INITIAL SETTLEMENT OF MARINE INVERTEBRATE LARVAE: THE ROLE OF PASSIVE SINKING IN A NEAR-BOTTOM TURBULENT FLOW ENVIRONMENT

by

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ABSTRACT

The hypothesis that planktonic larvae of benthic invertebrates sink through the water like passive particles in turbulent flows near the seabed was tested in the field using several groups of geometrically different sediment trap designs. A priori predictions regarding the rank order that the various traps would collect larvae in the field were dictated from laboratory flume experiments to determine the relative particle collection efficiencies of traps. The flume flow was seeded with particles having fall velocities similar to those measured, in the laboratory, for nonswimming polychaete larvae. The flume flow speed (of ~ 10 cm/sec) was within the range of near-bottom current velocities measured during trap collecting intervals at the study site.

In seven field experiments, each lasting from one to eleven days, trap collections of Mediomastus ambiseta (a polychaete worm) postlarvae, total bivalve larvae and postlarvae, sabellariid polychaete larvae, and enteropneust postlarvae generally fit the patterns predicted for passive particle collections between or among the trap designs. While the results were statistically more significant during some intervals than during others, the rank order of larval collections within each group of trap designs tested nearly always corresponded precisely to the rank order of passive particle collections by the traps in the flume experiments. Thus, the hypothesis that larvae sinking toward the seabed in the field and passive particles (with fall velocities similar to larvae) sinking in a flume are collected in the same rank order of abundance by near-bottom traps could not be falsified for collections of organisms from three invertebrate phyla.

Collections of the polychaete, Pectinaria gouldii, and of metamorphosing seastar larvae between or among trap designs significantly differed from the patterns predicted for passive particle collections. A testable hypothesis to explain the Pectinaria collections involves unique hydrodynamic properties of these postlarvae, relative to the other organisms collected, and is consistent with the passive sinking

ABSTRACT (cont.)

hypothesis. Trap collections of the seastars may have resulted, at least in part, from larvae adhering to solid trap surfaces during metamorphosis.

The passive sinking hypothesis could not be falsified in most of the field experiments conducted in this study. Thus, hydrodynamical processes must be included in any future studies of processes that determine patterns of larval settlement. However, passive sinking by larvae is not the explicit result of this experimental study. Other processes that could have produced the observed patterns of larval collections among the trap designs now must be tested against the passive sinking alternative hypothesis. However, much more information on the biology and ecology of the larvae collected in this study is required before future process-oriented experiments can be designed.

If larvae sink like passive particles to heights of ~ 50-cm above the seabed, as the results of this study suggest, then it is possible that larvae initially reach the seafloor at sites where particulates, with fall velocities similar to larvae, initially settle. This hypothesis requires experimental testing. Larvae may not remain at these initial settlement sites; however, after larvae initially reach the seafloor via passive physical processes, the larvae may redistribute by actively choosing a preferred microenvironment within that location, by actively swimming above the bottom or remaining on the sediment surface to be resuspended and transported away, by resuspension only during storm events, and/or by passively accumulating around microtopographic structures.

As a precursor to the flume tests of traps, a theoretical analysis of the physical nature of trap biases was conducted. A dimensional analysis of the independent variables involved in the process of trapping particulates suggested that trap collection efficiencies should be a function primarily of trap Reynolds number, trap aspect ratio, the ratio of the fluid velocity to the particle fall velocity, and trap geometry. A review of data from previous studies that flume-tested various trap designs further suggested that particle collection efficiencies of cylindrical traps should decrease over some range of increasing trap Reynolds number, decrease over some range of decreasing particle fall velocity and increase over some range of increasing trap aspect ratio. Theoretical models were then provided to account for these effects. Flume tests, in the present study, of cylinders varying by one order of magnitude in trap Reynolds number supported one of the predictions: particle collection efficiencies of the cylinders decreased by a factor of two over this range of increasing trap Reynolds number. Results of this theoretical and experimental study of trap collection characteristics suggest that more flume experiments to quantitatively determine the nature of trap biases are required before flux estimates, using traps in the field, can be adequately interpreted.

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BIOGRAPHICAL NOTE

The author was born on 26 November 1954 in Albany, California and was raised in Concord, California where she graduated from Clayton Valley High School in June 1972. She then attended San Jose State University (San Jose, CA), studying both botany and zoology, and eventually graduated with a B.A. in Zoology in June 1976. The scale was tipped toward invertebrate zoology during her last year at S.J.S.U. when she was the curator for the Invertebrate Zoology Museum at the University. From June 1976 through August 1978, the author attended Moss Landing Marine Laboratories (Moss Landing, CA) and S.J.S.U. in a Master's program while simultaneously coordinating a research grant, funded by the California State Water Resources Control Board, to design methods for using life history analyses of benthic invertebrates to monitor marine pollution. One aspect of this study, testing the feasibility of the life history approach at a local marine sewer outfall, constituted her Master's thesis research for which she obtained an M.A. in Biology (Marine) in May 1980. She was admitted to the W.H.O.I./M.I.T. Joint Program in Biological Oceanography in September 1978. After studying primarily physics and math during her first two years at M.I.T., it was possible for her to conduct interdisciplinary research on the role of small-scale hydrodynamical processes in determining sites for initial settlement of invertebrate larvae onto the seabed. During the spring of 1981, the author also taught a semester course in General Marine Ecology to undergraduates at Yale University. The author has accepted a position as a Postdoctoral Investigator at W.H.O.I. in the Ocean Engineering Department.

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LIST OF PRINCIPAL SYMBOLS

A_b	=	Area of trap bottom (general case)
A_m	=	Area of trap mouth (general case)
A_t	=	Trap mouth area (based on the inside diameter)
B_f	=	The final measured weight of beads collected by a trap
B_p	=	The predicted weight of beads collected by a trap
B_t	=	The corrected weight of beads collected by a trap
B_w	=	The weight of beads contained in the water sample collected when a trap is initially uncapped at depth
C	=	Centigrade
C_{ap}	=	Mean concentration of all particles (background particles and beads) in the flume during a trap collecting interval
C_{bp}	=	Mean concentration of background particles in the flume during a series
C_D	=	Drag coefficient
C_i	=	Mean bead concentration during a trap collecting interval
C_m	=	Coefficient of added mass
C_o	=	Concentration of particles in flow outside a trap
C_p	=	Particle concentration (general case)
C_t	=	Concentration of particles inside a trap
CV	=	Coefficient of variation
d	=	Particle diameter
D	=	Trap mouth diameter
d_e	=	Eddy diameter
E	=	Particle collection efficiency of a trap
E_r	=	Relative particle collection efficiency of a trap
E_s	=	Mean particle collection efficiency of trap OPC8.5-2.7 during a given series (factor used to normalize each E to obtain E_r)
EST	=	Eastern Standard Time
f	=	Function
g	=	Acceleration due to gravity

LIST OF PRINCIPAL SYMBOLS (cont.)

H	=	Trap height
H_a	=	Alternative hypothesis
H_o	=	Null hypothesis
L	=	Characteristic length scale
M	=	Characteristic mass scale
N	=	Total number of observations
N_c	=	Number of concentration of particles in the fluid
NL	=	Narcotized length of a larva
NW	=	Narcotized width of a larva
P	=	Particle trapping rate
ppt	=	Part per thousand
Q	=	Volume flux of fluid through a trap
r	=	Radius
R_f	=	Flow Reynolds number
r_o	=	Center of particle orbit inside an eddy
R_o	=	Radius of particle orbit inside an eddy
R_p	=	Particle Reynolds number
r_s	=	Spearman rank correlation coefficient
R_t	=	Trap Reynolds number
S	=	Ratio of particle density to fluid density
SD	=	Standard deviation
t	=	Time
T	=	Characteristic time scale
T_a	=	Response time of particle to fluid acceleration
t_c	=	Time required for particles to aggregate by shear collision
t_f	=	Residence time of fluid inside a trap
T_i	=	Length of a trap collecting interval
T_r	=	Time required for a sphere to reach terminal fall speed
t_s	=	Shear time scale
u	=	Mean stream flow speed
u_f	=	Flow speed at height of trap mouth
$\vec{u}_f$	=	Fluid velocity (general case)

LIST OF PRINCIPAL SYMBOLS (cont.)

$\vec{u}_{ip}$	=	Inertial velocity of a particle
$\vec{u}_p$	=	Particle velocity
V	=	Characteristic velocity scale
V_t	=	Trap volume
W	=	Fall speed (general case)
$\vec{W}$	=	Fall velocity
W_c	=	Calculated fall speed
W_m	=	Measured fall speed
x	=	Downstream distance from leading edge of a flat plate or, in this study, the flume basin (running coordinate for calculating δ)
$\bar{x}$	=	Mean
x_o	=	Point where a particle is entrained in an eddy
z	=	Vertical distance
α	=	Signifance level for a statistical test; the probability of rejecting a true H_o
β	=	Statistically, the probability of accepting a false H_o
δ	=	Boundary-layer thickness
ε	=	Rate of turbulent dissipation
μ_f	=	Fluid viscosity
ν	=	Kinematic fluid viscosity
ρ_f	=	Fluid density
ρ_p	=	Particle density
ϕ_b	=	Mass flux of particles resuspended from trap bottom
ω	=	Angular velocity

1. INTRODUCTION AND REVIEW OF THE LITERATURE

Dispersal of most soft-sediment marine invertebrates occurs during a planktonic larval stage. Planktonic larvae drift with currents for variable periods of time (hours to several months) before settling onto the sediment surface and assuming a benthic existence. Defining the physically-controlled and the biologically-controlled phases of the larval settlement process is necessary for determining the relative importance of larval settlement to establishing, maintaining and regulating benthic communities. In particular, the role of small-scale ($\leq$ tens of meters) hydrodynamical processes must be established because sediment types and benthic biological assemblages are most often distinguished at these spatial scales. While large-scale ($\geq$ tens of kilometers) larval dispersal has been assumed primarily a passive process controlled by general oceanic circulation (e.g., Crisp and Southward 1953; Thorson 1961; Scheltema 1971; Kraueter 1974; Levin 1983), larval settlement at very small spatial scales ($\leq$ centimeters) has been presumed primarily an active process where larvae choose the substrate most suitable for settlement (see reviews by Crisp 1974; Gray 1974; Scheltema 1974; Strathmann 1978; also the recent studies of Oliver 1979; Williams 1980; Gallagher et al., 1983). However, the relationship between small-scale hydrodynamical processes and patterns of initial larval settlement is largely undetermined.

The hypothesis that larvae fall through the water like passive particles in turbulent near-bottom flows has not been adequately considered. If larvae do act like passive particles in flows close to the seabed, then larvae may be initially deposited on the bottom at sites

where fine sediments (with fall velocities similar to larvae) initially settle. Hereafter, this is referred to as the "passive deposition hypothesis".

A test of the hypothesis that larvae act like passive particles in small-scale turbulent flows near the seabed is presented here. Due to complex biological and physical processes occurring once larvae have settled on the bottom, the passive deposition hypothesis cannot be tested by directly sampling the seabed for initially deposited larvae and inert particles. Thus, the intent of the present study was to determine if larvae that are capable of settlement (sensu Scheltema 1974, "the termination of a pelagic, larval existence and the assumption of a sessile or nonsessile sedentary life") act like passive particles while suspended in typical turbulent near-bottom flows.

The experimental approach in the present study involved using the biased sampling characteristics of sediment traps to collect particles and larvae falling toward the sediment surface. Traps differentially collect sediments because of self-induced local disturbances to the flow field; this effect is dependent upon trap geometry so that traps of various shapes will collect passive particles in different relative abundances. If larvae act like passive particles in near-bottom flows, then larvae and particles (with fall velocities similar to larvae) should be collected in the same relative abundances by the traps. If larvae are not collected according to the patterns predicted for passive particles, then other processes (e.g., biological features of the larvae such as behaviors or physiological responses) are governing the falling of larvae through near-bottom waters and the collection of larvae by traps.

Testing the hypothesis that larvae sink like passive particles in turbulent near-bottom flows is necessary for determining the likelihood that larvae fall like passive particles onto the seabed, initially reaching the seafloor at sites where fine sediments initially settle.

1.1 Research Components to and Organization of this Thesis

The three basic components to this research, presented in Chapters Two, Three and Four of this thesis, are described briefly below. In addition, the interdependence of the three chapters is discussed. A summary of the results of the entire study is presented in Chapter Five.

A theoretical discussion of the hydrodynamical processes governing particle collection by sediment traps in near-bottom turbulent flows is presented in Chapter Two (an analysis of particle behavior in accelerating flows is presented in Appendix I). This analysis was necessary because, (1) previous theoretical or experimental studies of sediment trap collection efficiencies did not cover the range of flows or particle types commonly encountered in coastal ocean environments; (2) understanding the nature of flow processes distributing and depositing sediments into traps indicates the nature of the flow processes to which larvae may respond; (3) a theoretical analysis of the hydrodynamics of particle trapping indicates the kinds of trap geometries likely to give the biased trapping effects desired in the present study (the relative particle collection efficiences of these trap geometries were then determined

in the laboratory flume study presented in Chapter Three); (4) determining which parameters primarily control the physics of particle trapping was necessary to design and conduct the flume study (Chapter Three) so that dynamic and geometric similarity to conditions during field experiments (Chapter Four) was maintained.

All laboratory measurements are presented in Chapter Three. First, fall velocities of nonswimming (anesthetized or freshly killed) invertebrate larvae were experimentally determined in a temperature-controlled water column. Second, a laboratory flume study was conducted to determine the particle collection efficiencies of various trap designs in a turbulent flow regime. The trap designs tested were dictated, in part, by the theoretical analysis of particle trapping (Chapter Two). The mean flow speed in the flume was within the range of flow speeds measured at the height of the trap mouths during field experiments (Chapter Four). The passive particles chosen for the flume study had fall velocities within the range of those directly measured for larvae. The primary purpose of the flume study was to identify pairs or groups of trap types that collected passive particles in different relative abundances (i.e., one trap design overcollecting particles relative to the other trap design). These measurements were used to form specific a priori hypotheses regarding larval collections in the field. Thus, the flume study dictated which trap designs were used in the field to test the hypothesis that larvae are passively collected in traps in the same relative abundances that the traps collected passive particles in the flume. A secondary purpose of the flume study was

to experimentally investigate the nature of sediment trap biases in turbulent flows; some of the theoretical predictions of trapping bias (Chapter Two) were tested. Because this portion of the flume study was not related directly to the basic biological question of this thesis, results of these experiments are presented in Appendix II. The raw data for all particle collection efficiency calculations of all traps tested are given in Appendix III.

Chapter Four presents all results of the field component to this study. Twenty different trap designs were deployed in 17 field experiments (usually only 2 or 3 designs were tested simultaneously) to test the hypothesis that larvae act like passive particles in near-bottom turbulent flows. Results of seven of these experiments are discussed in Chapter Four. Field experiments were carried out in a shallow subtidal (15-m depth) region of Buzzards Bay, MA, from July through September in 1980 and from July through October in 1982. Results of the flume study (Chapter Three) were used to predict collections of larvae by traps during both sets of field experiments. During the 1982 experiments, Dr. Bradford Butman of the U.S. Geological Survey (Woods Hole, MA) deployed a bottom tripod system at the study site to record near-bottom current velocity and direction (at the height of the trap mouths), pressure, temperature, and light transmission during experiments. The physical measurements of flows near the seabed are integrated with results of the trap experiments for a complete discussion of the settling of larvae through the water in near-bottom turbulent flows. The implications of these results to initial deposition of larvae onto the seabed

are also discussed. Results of four of the field experiments, using the two trap designs most commonly deployed in this study, were analyzed as a unit and submitted for publication; the manuscript appears as Appendix IV. These results also are presented and discussed in greater detail in Chapter Four.

1.2 Review of Soft-Bottom Larval Settlement Studies

Little is known about how initial patterns of larval settlement relate to the eventual distributions of adults. Field studies to determine mechanisms controlling benthic community structure usually did not consider larval settlement phenomena. Even when larval settlement was included in analyses, the studies were rarely designed so that differential larval settlement could be distinguished from differential post-settlement mortality. Studies designed to determine mechanisms controlling larval settlement overwhelmingly favor the active habitat selection hypothesis; however, most of these studies did not consider or test the alternative hypothesis that larvae are passively deposited onto the seabed. Whether or not larval settlement sites in the field are determined by passive physical processes has been largely a matter of data interpretation. However, the few field studies which experimentally tested the passive deposition hypothesis demonstrated that it is a feasible alternative explanation for patterns of larval settlement and infaunal recruitment.

This review is limited to settlement of larvae of soft-bottom infaunal invertebrates. Woodin and Jackson (1979) discuss

differences between hard- and soft-substrate environments to which larvae may respond; these differences are outlined below. Settlement of hard-substrate organisms (e.g., barnacles, spirorbid polychaetes, and bryozoans) usually involves sensing and responding to only two-dimensional surfaces. The organisms fix themselves permanently or semi-permanently to these surfaces with various secretions. Sediments are three-dimensional environments where organisms can respond behaviorally and physiologically not only to the two-dimensional sediment surface, but may be adapted to the third dimension, subsurface properties of sediments, as well.

The physical behavior of planktonic stages of organisms in fluid flows is probably more segregated by size and taxonomic position than by the nature of the substrate on or in which the organisms live. Clearly, some groups of organisms (e.g., crustaceans, squid, and scallops) possess orders of magnitude better swimming abilities than other groups (e.g., polychaetes) (see review by Mileikovsky 1973). For considerations of passive transport, the size of the organism and its fall velocity are the most important considerations (see Chapter Two). Thus, in discussions of water column processes, I include all organisms within the size range of infaunal larvae, but regarding settlement onto the seabed I limit the discussion to soft-bottom infaunal organisms.

1.2.1 Definition of terms

For clarity, the definitions of some terms commonly used in larval studies are reiterated here. Planktonic larvae of infaunal invertebrates undergo larval development in the water column during

the "dispersal" phase of their life histories. Dispersal is entirely a water column phenomena; larvae are generally considered to be developing and not ready to settle during dispersal. Dispersing planktonic larvae are easy to identify in certain groups, such as the Crustacea, where several distinct larval stages precede a final larval form that can settle onto the substrate. In other groups, such as the Polychaeta, larval development usually involves the gradual addition of segments and loss of ciliation; cessation of planktonic development and thus, of the dispersal phase, may be more difficult to identify in these groups.

Dispersal is largely regarded as passive transport by water currents because the scales of horizontal water motion are so much greater than the swim speeds of larvae (see Mileikovsky 1973). However, active behavioral and physiological responses of larvae (e.g., phototaxis, geotaxis, and responses to salinity changes) may displace them vertically where the scales of water motion may not be large compared to the movements of the larvae (Mileikovsky 1973). Thus, there may be an active component to passive dispersal of larvae because the organisms could voluntarily make vertical migrations into particular water masses. The relative contribution of active larval behaviors versus passive transport processes for the retention of larvae in estuaries has been debated for several decades (e.g., Bousfield 1955; Wood and Hargis 1971; deWolf 1974, 1981; Cronin and Forward 1979; Sulkin and van Heukelem 1981).

The present study does not address large scale larval dispersal but is concerned with the movements of planktonic larvae in waters

close to (within 1.5 m of) the seabed. It could be argued that these larvae are still dispersing, but over smaller spatial scales. However, most of the larvae sampled in the present study were ready to settle (that is, "available" for settlement, see below) so, strictly speaking, they were no longer in the dispersal phase of their life histories.

Larval "development" was separated into two periods for planktonic larvae of the gastropod, Nassarius obsoletus Say, by Scheltema (1967): a "development period" during which growth and differentiation of the larva occurs and a "delay period" during which there is a gradual decrease in growth and the larva is physiologically capable of "metamorphosis". During "metamorphosis", an organism undergoes certain morphological and physiological changes that "portend a new way of life" (Scheltema 1974). Usually, larvae considered "available" for settlement ("settlement" was defined in the introductory remarks to this chapter) includes only larvae that have entered the delay period of their planktonic development. Unfortunately, for many polychaete species this is difficult to determine, except ex post facto. For example, polychaete larvae were considered available for settlement in the study of Hannan (1981) if they had undergone metamorphosis by the time they were collected in near-bottom sediment traps. Even in laboratory experiments, it is difficult to determine if an unmetamorphosed larva is capable of metamorphosis because once the organism has passed through the development period, it may require a specific cue for metamorphosis to occur (see reviews by Wilson 1958; Thorson 1966; Meadows and

Campbell 1972; Scheltema 1974; Crisp 1974; Strathmann 1978). Nonetheless, in the present study, I will abide by the definition of "available" larvae being only those within the delay period of their planktonic larval development.

It is important to clearly distinguish between metamorphosis, settlement, and "recruitment". Metamorphosis may preceed, correspond with, or follow settlement and refers to an irreversible set of anatomical and physiological changes in the organism presumably "coordinated through an endocrine mechanism" (Scheltema 1974). Metamorphosed larvae are called "postlarvae" in the present study. Settlement "denotes a responsive behaviour" and is "presumed to be under nervous control" (Scheltema 1974). This is not to say that settling onto the sediment surface is, by definition, an active choice by the larva. I interpret Scheltema's (1974) definition to mean that by "settling", a set of behaviors (e.g., burrowing and tube building) are triggered which are indicative of the benthic life history stage of the organism. Thus, where metamorphosis marks the morphological change from a larval to a postlarval form, settlement marks a change in venue from a planktonic to a benthic existence. Unfortunately, this definition of settlement implies that once settled, the organism will not again occur in the water column but will preside entirely in or on sediments. In this regard, Scheltema's (1974) definition of settlement must be modified because a volumninous literature records the occurrences of postlarval and adult benthic organisms in the water column (see Table 1.1).

In contrast to dispersal, metamorphosis, and settlement,

TABLE 1.1

Observations of Benthic Postlarval and Adult Polychaetes, Molluscs and Meiofauna in the Water Column[1]

Reference	Method of Observation	Organisms Observed
Bayne (1964)	plankton tows	Mytilus edulis Linnaeus (B)
Emery (1968)	plankton tows; suction devices	nereids and other polychaetes
Seymour (1972)	laboratory observations (but cites Fage and Legendre 1927 for field observations)	Arenicola marina Lamarck (NS)
Thomas and Jelley (1972)	emergence traps	Eteone lactea Claparede Glycera dibranchiate Leidy Nereis succinea (Frey and Leukart) (I, A, S) Nereis virens Sars (I, A, S) Pherusa affinis (Leidy) Scoloplos fragilis (Verrill) (F, S)
Beukema (1973)	plankton tows	Macoma balthica (Linnaeus) (B)
Porter (1974)	plankton tows	polychaetes (A)
Hobson and Chess (1976)	plankton tows	polychaetes
Alldredge and King (1977)	emergence traps; plankton tows	polychaetes from the Families: Syllidae Orbiniidae Opheliidae
Porter and Porter (1977)	emergence traps	polychaetes
Porter et al. (1977)	emergence traps	polychaetes

TABLE 1.1 (cont. - 2)

Reference	Method of Observation	Organisms Observed
Dean (1978a)	direct observations of surface waters at night with searchlight; specimens collected with dipnet	Nereis virens (Sars) (I)
Dean (1978b)	direct observations of surface waters at night with searchlight; buoyed and anchored nets	Glycera dibranchiata Leidy (I) Glycera capitata Oersted (I) Eteone longa Claparede (F) Nephtys discors Ehlers Glycera sp. (I) Nereis virens Sars Pherusa affinis (Leidy)
Graham and Creaser (1978)	buoyed and anchored plankton nets	Glycera dibranchiata Leidy (A, NS)
Beukema and DeVlas (1979)	plankton tows	Arenicola marina Lamarck (I)
Hobson and Chess (1979)	emergence traps	polychaetes
Alldredge and King (1980)	emergence traps	Brania sp. (F, S) Sphaerosyllis hystrix Claparede (F, S) Armandia brevis Moore (A, NE) Aricidea sp. (A) Prionospio heterobranchiata newportensis Reish (A) Pseudoeurythoe sp. (A) Gyptis brevipalpa Hartman-Schroder (A) Protodorvillea gracilis Hartmann (A) Nematonereis unicornis Grube (A)
Bell and Sherman (1980)	samples of water overlying sediments	meiofauna
Dauer et al. (1980)	plankton tows; direct observations of surface waters	Scolecolepides viridis (Verrill) (I, A, S)

TABLE 1.1 (cont. - 3)

Reference	Method of Observation	Organisms Observed
Santos and Simon (1980a)	containers filled with sediment raised 0.5-m above bottom	Nereis succinea (Frey and Leukart) (A) Gyptis vittata Webster and Benedict (A) Parahesione luteola (Webster) Stylochus sp.
Bhaud et al. (1981)	near-bottom sediment traps	Phyllodoce sp. (I or A) Polydora antennata Claparede (I or A) Spio martinensis Mesnil (I or A) Amphictenidae (I or A) Polyophthalmus pictus (Dujardin) (I or A) Syllidae germiphores (I or A) Ophryotrocha sp. (I or A) "lamellibranchs" (B, I or A)
Hagerman and Rieger (1981)	sediment traps	meiofauna meiobenthic polychaetes
Levin and Greenblatt (1981)	plankton tows	Loimia sp. (I)
Tranter et al. (1981)	downward-directed light traps	polychaetes
Dobbs and Vozarik (1983)	filtrate from power plant cooling system	polychaetes (47 species) bivalves (7 species) gastropods (12 species)

1. Some studies may have collected larval forms along with immature and adult organisms; this information usually was not given in the paper. In this table, when information on the state of maturation of the collected organisms was given in the paper, the name of the organism is followed by: A = adult, NS = nonspawners, S = some indiviudals may have been spawning, I = immatures, F = female with eggs, NE = not epitokous. All species listed are polychaetes, unless noted (B = bivalve).

"recruitment" is not a real stage in the life history of the organism but is observer-defined; the organisms surviving to a size collected by the observer are considered "recruited" individuals (Keough and Downes 1982). Because recruitment is defined basically by the sieve screen size and the sampling interval in infaunal studies, recruited organisms can be unmetamorphosed larvae, postlarvae, juveniles, or adult organisms. However, settlement refers only to larvae (or, when larvae metamorphose prior to settlement, postlarvae) (Keough and Downes 1982).

By these definitions, in order to study settlement, the first larval stages to reach the seabed and begin living as benthic organisms must be sampled; to emphasize this fact, in the present study I refer to these as "initially settled" larvae. As Keough and Downes (1982) pointed out, most studies which claim to measure larval settlement have actually measured recruitment.

1.2.2 Benthic surveys and process-oriented field studies have focused on processes affecting postlarval and adult organisms

Early studies of benthic communities were primarily surveys that compared sediment distributions with distributions of postlarvae and adult infauna over areas of the seafloor. The general observation that species distributions are often well-correlated with distributions of particular sediment grain sizes (Table 1.2, but see also conclusions of McNulty et al., 1962b; Santos and Simon 1974) dates back to the earliest quantitative studies of marine benthic communities (e.g., Peterson 1918). Detailed studies of the feeding

TABLE 1.2

Benthic Survey Studies of Infauna and Sediment Distributions Over Areas of the Seafloor[1]

Reference	Location of Study	Depth (meters)	Sieve Screen Size (microns)	Minimum Sampling Interval	Minimum Distance Between Stations (meters)
Ford (1923)	Plymouth, England	ING	"series of screens"	Sampled Once	123
Sparck (1933)	Franz Joseph Fjord, East Greenland	27-780	ING	Sampled Once	730
Stephen (1933)	Northern North Sea, Scotland	0-200	1500, 2000	Sampled Once	ING
Thorson and Ussing (1934)	Scoresby Sound Fjord Complex, East Greenland	20-530	ING	Sampled Once	1760
Holme (1949)	Mouth of Exe Estuary, England	Intertidal	1000	Sampled once	30
Sanders (1956)	Long Island Sound, NY	6-31	300, 2000	2 months	3220
Sanders (1958)	Buzzards Bay, MA	7-20	500	Sampled once	1850
Wieser (1959)	Puget Sound, WA	Intertidal	Not sieved	Sampled once	ING
McNulty (1962a)	Biscayne Bay, FL	2-10	1000	Sampled once	230
Sanders et al. (1962)	Barnstable Harbor, MA	Intertidal	Unscreened, 750	1 year	ING

TABLE 1.2 (cont. - 2)

Reference	Location of Study	Depth (meters)	Sieve Screen Size (microns)	Minimum Sampling Interval	Minimum Distance Between Stations (meters)
Buchanan (1963)	Coast of Northumberland, North Sea	10-90	ING	Sampled once	1800
Gray (1968)	Eagle Cove, San Juan Island, WA	Intertidal	"fine plankton net"	1.5 months	10
Lie (1968)	Puget Sound, WA	12-200	1000	2 months	2000
Gibbs (1969)	Plymouth Sound, England	2-12	500	Sampled once	50
Nichols (1970)	Port Madison, Puget Sound, WA	2-34	1000	Sampled once	75
Day et al. (1971)	Beaufort Shelf, NC	0-200	1000	2 months	1110
Johnson (1971)	Tomales Bay, CA	0-18.5	1500	ING	ING
Bloom et al. (1972)	Tampa Bay, FL	Intertidal	1000	4 months	20
Gage (1972)	Lochs Etive and Crenan, Sweden	0-117	1000	Sampled once	710
Eagle (1973)	Liverpool Bay, England	5-11	500, 1000	5 months	310
Gage and Geekie (1973b)	Loch Etive, Sweden	20-60	1000	Sampled once	100

TABLE 1.2 (cont. - 3)

Reference	Location of Study	Depth (meters)	Sieve Screen Size (microns)	Minimum Sampling Interval	Minimum Distance Between Stations (meters)
Santos and Simon (1974)	Tampa Bay, FL	Intertidal	500	3 months	90
Mountford et al. (1977)	Chesapeake Bay, MD	3-9	1000	3 months	280
Tyler and Banner (1977)	Oxwich Bay, Bristol Channel, Wales	5-20	1000	Sampled once	55
Whitlatch (1977)	Barnstable Harbor, MA	Intertidal	250	1 month	65
Larsen (1979)	Sheepscot Estuary, ME	0-9	1000	Sampled once	ING
Flint and Holland (1980)	Gulf of Mexico, TX	22-131	500	1 month	6390
Shin and Thompson (1982)	Coastal waters of Hong Kong	13-70	400	2 months	500

1. The intent of this table is to give a historical account of the sampling scales, sampling intervals and sieve screen sizes used in a selection of survey studies (where benthic communities and sediments were sampled simultaneously). The list is intended to be illustrative, not exhaustive. Minimum distances between stations were usually estimated from plots of station locations on maps of the study sites. ING = Information not given in the reference; Sampled once = each station was sampled once only and not necessarily simultaneously with the sampling of the other stations.

and mobility types of the infauna revealed that functional groups of organisms occurred in distinct sediment types. Most authors did not speculate on larval settlement mechanisms which could have produced these patterns of distribution, but only discussed the favorability of these particular habitats to adults. The most popular explanation for these assemblages concerned the availability of food resources. For example, Sanders (1958) hypothesized that deposit feeders dominate clays because these sediments are also rich in organics and microbes while filter-feeders prefer sandier environments because the higher near-bottom flows maintain particulates in suspension for food.

A process-oriented approach to studying patterns of species distributions in soft-bottom environments began with the landmark study of Rhoads and Young (1970). They experimentally demonstrated the feasibility of the "trophic amensalism" hypothesis (activities of deposit feeding organisms interfere with the establishment and maintenance of populations of suspension feeders). In addition, they showed that amensalistic interactions are intimately related to the nature of the sedimentary environment (e.g., the degree of substrate motion). However, Rhoads and Young (1970) and subsequent experimental studies of competition, predation and animal/sediment interactions (Table 1.3 and reviews by Gray 1974; Rhoads 1974) failed to consider how the functional groups of organisms are initially established. The studies did not determine if distinct assemblages resulted from differential larval settlement or differential post-settlement mortality, nor did they consider how the mechanisms controlling larval settlement (e.g., active habitat selection or

TABLE 1.3

Process-Oriented Field Studies of Factors Controlling Soft-Bottom Community Structure; Studies Arranged by the Process Under Investigation[1]

Reference	Minimum Sampling Interval	Sieve Screen Size (microns)
COLONIZATION, SUCCESSION, RESPONSE TO DISTURBANCE		
Grassle and Grassle (1974)	2 days	297
Boesch et al. (1976)	3 months	500, 1000
Dauer and Simon (1976)	1 month	500
McCall (1977)	1 month	297, 1000
Rees et al. (1977)	1 month	1000
Rhoads et al.(1977)	2 months	300, 1000
VanBlaricom (1978)	1 week	500
Woodin (1978a)	1 month	1000
Oliver et al. (1980)	1 month	500
Santos and Bloom (1980)	1 month	500
Santos and Simon (1980a)	1 week	250, 500
Santos and Simon (1980b)	1 month	500
PREDATION		
Young et al. (1976)	1 month	1000
Reise (1978)	2 weeks	500, 1000, NS
Virnstein (1978)	2 months	500
Arntz (1980)	2 months	1000
Holland et al. (1980)	2 months	500
Hulberg and Oliver (1980)	2 months	250, 500
ANIMAL-SEDIMENT RELATIONS		
Rhoads and Young (1970)	1 month	500, 1000
Young and Rhoads (1971)	Sampled once	1000
Levinton (1977)	1 year	2000
Myers (1977a, 1977b)	1 week	500
Orth (1977)	1 month	1000
Wilson (1979)	1 month	500
Brenchley (1981)	7 days	500
Wilson (1981)	1 year	500
COMPETITION		
Woodin (1974)	1 month	500, 1000
Peterson (1977)	1 day	2300
Weinberg (1979)	1 month	500
Peterson and Andre (1980)	55 days	2300
Wilson (1983)	1 week	500

TABLE 1.3 (cont. - 2)

Reference	Minimum Sampling Interval	Sieve Screen Size (microns)
TEMPORAL VARIABILTIY		
Muus (1967)	1 month	700, 1000, NS
Lie (1968)	2 months	1000
Dauer and Simon (1975)	3 months	500
Holland and Polgar (1976)	3 months	1000
Holland et al. (1977)	3 months	1000
Whitlatch (1977)	1 month	250
Buchanan et al. (1978)	2 months	500

1. Studies chosen for inclusion in this table were those that investigated processes structuring macrofaunal communities; studies concerned with factors controlling abundances of only an individual population were not included. This list includes the commonly cited studies in the English literature and is not intended to be comprehensive. NS = some of the samples were not sieved.

passive deposition) would effect the establishment and maintenance of the assemblages (Dayton and Oliver 1980 discuss these problems).

Errors in data interpretation may result if larval processes are not considered in analyses. For example, if initial distributions of larvae on the seabed result from differential larval settlement, then larvae must actively select their settlement sites for Rhoads and Young's (1970) trophic amensalism hypothesis to be upheld. If differential larval settlement results from passive deposition (depending on larval fall velocities and on the near-bottom flow regime), then it may not be necessary to evoke complex amensalistic interactions to explain the distributions of organisms. That is, suspension feeders may not co-occur with deposit feeders simply because the two functional groups have larvae with different fall velocities that are passively deposited in different environments. If larvae are passively deposited over large areas of the seabed, distinct assemblages occurring over smaller spatial scales may result from differential post-settlement mortality or from other post-settlement phenomena (e.g., active habitat selection at small spatial scales). Mechanisms (e.g., competition or predation) responsible for these post-settlement processes then must be examined. This example illustrates the necessity for sampling initially settled larvae and for understanding the mechanisms responsible for these settlement patterns so that results of process-oriented studies of community structure will not be misinterpreted.

1.2.3 Methodological problems with field studies: Larval stages usually were not collected

In both the survey and the process-oriented studies of soft-bottom community structure, the importance of larval ecology could not even be assessed *a posteriori* because larvae were rarely quantitatively collected in samples (Tables 1.2 and 1.3). Two methodological problems have especially prohibited an adequate consideration of the larval stages (Dayton and Oliver 1980; Santos and Simon 1980a; and Williams 1980 discuss these problems). (1) Field sampling was usually too infrequent (monthly or even biweekly) to record *initial* settlement prior to post-settlement interactions. (2) The sieve size (500 μm) commonly used in recent benthic studies is too large to retain newly settled larvae of many invertebrate species. When Eckman (1979) used nested sieves to determine the smallest screen size required to retain newly settled larvae of particular invertebrate species, use of even a 250-μm or a 300-μm screen resulted in severe losses of larvae: Eckman (1979) determined that a 61-μm screen was necessary to retain the smallest postlarvae of several polychaetes and crustaceans at Skagit tidal flat in Puget Sound, WA and, in the present study, 94 percent of the newly settled *Mediomastus ambiseta* (Hartman) larvae were retained on 100-μm screens, while only six percent were found on the 300- and 500-μm screens combined (see Table 4.3). Gallagher et al. (1983) measured dimensions of smallest recruits of the dominant Skagit flat infauna. All newly settled polychaetes, oligochaetes and crustaceans could easily pass through a 250-μm sieve, while the smallest recruits of

one polychaete species, Hobsonia florida (Hartman), and the oligochaetes could pass through even a 100-μm sieve.

1.2.4 Active habitat selection hypothesis favored, but passive deposition hypothesis rarely considered

In all discussions of the role of larval settlement in soft-bottom community ecology (e.g., Thorson 1946, 1950, 1957, 1966; Smidt 1951; Muus 1973; Gray 1974; Woodin 1976; Woodin 1978b; Oliver 1979; Woodin and Jackson 1979; Dayton and Oliver 1980), active habitat selection by larvae is the favored mechanism for establishing and maintaining benthic communities. Support for this hypothesis comes from the numerous laboratory experiments where larvae were given a choice of substrates in which to settle (Table 1.4 and reviews by Wilson 1958; Thorson 1966; Meadows and Campbell 1972; Crisp 1974; Gray 1974; Scheltema 1974; Strathmann 1978). However, Thorson (1966) suggested that larvae may not be as substrate selective in the field as they are in the laboratory so that larvae may settle in the first "acceptable" habitat they encounter. Post-settlement mortality may then play some role in determining the eventual distribution of adults (e.g., see Levinton and Bambach 1970). The field studies on larval recruitment by Muus (1973) and Oliver (1979) strongly support the active habitat selection hypothesis, but also suggest that differential post-settlement mortality further restricts the distribution of adults.

The conclusion that larvae actively select their settlement sites in the field is equivocal because results of larval choice experiments have been too liberally and uncritically applied directly

TABLE 1.4

Laboratory Experiments on Habitat Selection by Soft-Bottom Invertebrate Larvae, Juvenile or Adult Macrofauna, and Meiofauna[1]

Reference	Orgainsm(s) Studied	Maximum Dimension of Treatment (millimeters)	Maximum Distance Between Treatments (millimeters)
STUDIES OF MACROFAUNA LARVAE			
Wilson (1948)	Ophelia bicornis Savigny (P)	15	45
Wilson (1952, 1953a, 1953b, 1954, 1955)	Ophelia bicornis Savigny (P)	7.5	"a few cm"
Wilson (1970a)	Sabellaria alveolata (Linnaeus) (P)	17	30
Wilson (1970b)	Sabellaria spinulosa Leuckart (P)	17	30
Wilson (1977)	Lygdamis muratus (Allen) (P)	23	20
Keck et al. (1974)	Mercenaria mercenaria (Linne) (B)	ING[2]	ING
J.P. Grassle (pers. comm.)	Capitella spp. (Types I and II) (P)	40	80
STUDIES OF MEIOFAUNA AND JUVENILE OR ADULT MACROFAUNA			
Wieser (1956)	Cumella vulgaris Hart (C)	ING[3]	ING
Webb and Hill (1958)	Branchiostoma nigeriense Webb (L)	75	130
Williams (1958)	Penaeus setifeus (Linnaeus) (PS) Penaeus aztecus Ives (PS) Penaeus duorarum Burkenroad (PS)	457	1372
Meadows (1964a)	Corophium volutator (Pallas) (H)	90	160
	Corophium arenarium Crawford (H)	60	1-2*

TABLE 1.4 (cont. - 2)

Reference	Orgainsm(s) Studied	Maximum Dimension of Treatment (millimeters)	Maximum Distance Between Treatments (millimeters)
STUDIES OF MEIOFAUNA AND JUVENILE OR ADULT MACROFAUNA (Continued)			
Meadows (1964b)	Corophium volutator (Pallas) (H)	170	1-2*
Meadows (1964c)	Corophium volutator (Pallas) (H) Corophium arenarium Crawford (H)	60	1-2*
Gray (1966a)	Protodrilus symbioticus Giard (A)	20	50
Gray (1966b)	Protodrilus symbioticus Giard (A)	ING	ING
Gray (1966c)	Protodrilus symbioticus Giard (A)	10	50
Gray (1967a)	Protodrilus rubropharyngeus Jagersten (A)	20	50
Gray (1967b)	Protodrilus hypoleucus Armenante (A)	10	40
Jansson (1967a)	Parastenocaris vicesima Klie (H)	8	ING
Jansson (1967b)	Coelogynopora schulzii Meixner (T) Aktedrilus monospermatecus Knoller (TO)	8	ING
Gray (1968)	Leptastacus constrictus Lang (H)	10	50
Lewis (1968)	Fabricia sabella (Ehrenberg) (P)	64	1-2*
Sameoto (1969a)	Haustorius canadensis Bousfield (H) Neohaustorius biarticulatus Bousfield (H) Acanthohaustorius millsi Bousfield (H) Parahaustorius longinerus Bousfield (H) Protohaustorius deichmannae Bousfield (H)	67	1-2*
Gray and Johnson (1970)	Turbanella hyalina Schultze (G)	10	120

TABLE 1.4 (cont. - 3)

Reference	Orgainsm(s) Studied	Maximum Dimension of Treatment (millimeters)	Maximum Distance Between Treatments (millimeters)
STUDIES OF MEIOFAUNA AND JUVENILE OR ADULT MACROFAUNA (Continued)			
Hadl et al. (1970)	Microhedyle milaschewitchii Kowalevsky (O)	15	2
Gray (1971)	Scolelepis fuliginosa (Claparede) (P)	75	150
Jensen (1981)	Chromadorita tenuis (Schneider) (N)	100	90

1. Dimensions of treatments and distances between treatments are rough estimates because they were usually calculated, for this table, from the information available in the reference. *treatments adjacent to each other with some sort of partition between them; A = archiannelid, B = bivalve, C = cumacean, G = gastrotrich, H = haustoriid amphipod, N = nematode, O = ophisthobranch gastropod, PS = penaeid shrimp, T = turbellarian, TO = tubificid oligochaete, ING = information not given in paper
2. 64 blocks in 8 X 8 arrays in a 284-liter tank (other dimensions not given in paper)
3. "equal volumes of two kinds of substrata" in "Petri-dishes" (details not given in paper)

to field situations. Moore (1975), in a unique critical analysis of the possible role of active habitat selection in natural field environments, emphasized that organisms may not have the same kinds of "free choices" in the field as they have been given in the laboratory. He points out that, during dispersal, planktonic larvae are restricted to particular localities by passive transport processes so that larvae may never even encounter the preferred substrates (as determined in laboratory experiments) in the field. Post-settlement mortality or passive deposition of larvae may then shape species distributions. Most field studies have not carefully distinguished between differential larval settlement and differential post-settlement survival because initial larval settlement usually was not sampled (see Section 1.2.3). In addition, the simplest hypothesis for observed patterns of species distributions, that larvae are passively deposited onto the seabed as are the sediments characterizing a particular location, was not tested prior to evoking more complex biological explanations (e.g., active habitat selection) for the data.

Laboratory studies (Table 1.4 and reviews cited above) on active habitat selection by soft-bottom invertebrate larvae were done only in still water aquaria; the relevance of these results to field flows and turbulence is presently obscure. Several studies observed the ability of larvae or meiofauna to settle or remain attached to the substrate in laboratory water "currents". Wilson (1948) directed a small stream of water at individual larvae settling in a Petri dish and observed the organism's settlement response. Boaden (1963, 1968)

and Gray (1966b) observed the behavior of meiofauna in water flowing through a small space between parallel glass plates and through clear tubing containing individual organisms. Finally, Wilson (1968) quantitatively determined the settlement of larvae in "rough water" by using a plunger attached to a stirring motor to keep the water in laboratory dishes in motion. However, these were not habitat selection experiments, nor were any of these flows analogous to field flows near the seabed.

All field studies which used artificial structures to collect larvae (see Table 1.5) may just show a "trapping artifact" -- physical, chemical, and biological differences between the microenvironment of the trap and the natural bottom which complicate data interpretation (Oliver 1979 and Hannan 1981 discuss this problem for larvae collectors). Unless a priori predictions can be made regarding the specific hydrodynamical and biological disturbances created by these structures, then it is impossible to unambiguously interpret results from these experiments. Even results from field studies where bottom sediments were sampled directly (Muus 1966, 1973) or studies involving experimental manipulations (e.g., Oliver 1979; Williams 1980; Gallagher et al., 1983) are inconclusive because the passive deposition hypothesis was never tested. In all of the field studies, larvae could have been passively deposited or more efficiently collected in one environment than in another.

Differential larval settlement cannot be distinguished from differential post-settlement survival unless initial patterns of settlement in the field can be documented. Woodin (1976, 1978b)

TABLE 1.5

Field Experiments on Habitat Selection by Soft-Bottom Invertebrate Larvae, Juvenile or Adult Macrofauna and Meiofauna[1]

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
*Thorson (1946)	"bottle collectors" 2-m above seabed, also plankton tows, plankton pump and bottom samples	all infaunal larvae collected	6 weeks for bottles, 2 weeks for tows and pump	ING for bottles, 83 for tows and pump	ING	bottle dimensions not given	NA
*Reish (1961)	"sediment bottle collectors"	all organisms collected	28 days	246	710	"gallon jar", dimensions not given	NA
Boaden (1962)	manipulations of intertidal sediments	meiofauna	20 days	ING	OSO	5	ING
Hermans (1964)	different substrates placed in bottle collectors and suspended below low tide level	Armandia brevis Moore (P)	2 weeks	ING	OSO	"Thorson" bottles, dimensions not given	ING

TABLE 1.5 (cont. - 2)

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
*Muus (1966, 1973)	simultaneous samples of bottom and plankton at two subtidal locations	bivalves	2 weeks	265 for sediments, 180 for plankton	1000	NA	NA
Richter and Sarnthein (1977), but technical layout in Sarnthein and Richter (1974)	3 different substrates placed in trays moored 2- to 4-m above seafloor at 3 subtidal depths	molluscs	2 weeks	63	80 (maximum horizontal distance between depths)	71	118
Guerin and Masse (1978), Masse and Guerin (1978)	different substrates were placed in 3 designs of collectors moored on the bottom or 80-cm above the bottom at subtidal depths	polychaetes and molluscs	1 month	1000 "on diagonal" (= 700 if mesh is square)	ING	8.6	180

TABLE 1.5 (cont. - 3)

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
*VanBlaricom (1978)	replicate containers with small layer of sediment were moored above the seabed; bottom also sampled	all infauna	13 days for containers, 1 mouth for bottom	250 for containers, 500 for bottom		10 for containers	ING
Eckman (1979)	manipulations of intertidal sediments	all abundant infauna	11 days	61	OSO	100	700
Oliver (1979), Dayton and Oliver (1980)	(a) different treatments were placed in containers held in racks above subtidal seabed; bottom sampled simultaneously	polychaetes	(a) 6 days	(a) 250 for containers, 500 (250 for "a few cores") for bottom	(a) OSO	(a) 10 for containers	(a) 42 for containers
	(b) bottom sediments were also manipulated at 3 stations and sampled over a "disturbance gradient"		(b) 1 month	(b) 500 (250 for "a few cores")	(b) 1000	(b) > 2000	(b) ING (for distances between stations in "disturbance gradient")

TABLE 1.5 (cont. - 4)

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
*Santos and Simon (1980a)	containers filled with sediment were placed in rack above subtidal seabed, plankton tows and bottom samples were also collected	all infauna and settling larvae	7 days for containers, "irregularly" for tows, 1 month for bottom	OSO	250 for containers, 144 for tows, 500 for bottom	5 for containers	ING
Williams (1980)	manipulations of intertidal sediments	Tapes japonica (Reeve) (B)	7 days	149	OSO	150	750
*Bhaud et al. (1981)	collectors filled with sediment were placed 10- to 110-cm above subtidal seabed, also collected samples with epibenthic sledge	polychaetes and bivalves	5 days	ING	OSO	"2 liter capacity", dimensions not given	ING

TABLE 1.5 (cont. - 5)

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
*Hannan (1981)	replicate collectors with small layer of sediment were moored 1-m above subtidal seabed at two locations; seabed sampled simultaneously for larvae and macrofauna	Armandia brevis Moore (P), Capitella spp. (P), Nothria elegans Johnson (P) Prionospio pygmaea Hartman (P)	7 days for collectors and larval bottom cores, 1 month for macrofaunal bottom cores	250 for collectors and larval bottom cores, 500 for macrofaunal bottom cores	400	10	30 (between replicate collectors)
Levin (1981)	different sediment treatments filled containers that were placed directly on intertidal sediments; natural bottom sediments were also sampled	Streblospio benedicti (Webster)(P) Pseudopolydora paucibranchiata (Okuda) (P)	2 weeks	worms were visually counted under dissecting microscope	OSO	9	26

TABLE 1.5 (cont. - 6)

Reference	Experimental Approach	Organisms Studied	Minimum Sampling Interval	Sieve Screen Size (microns)	Minimum Distance Between Stations (meters)	Maximum Treatment Dimension (cm)	Maximum Distance Between Treatments (cm)
Eckman (1983)	manipulations of intertidal sediments	all abundant infauna	2 days	61	OSO	30	1970
Gallagher et al. (1983)	manipulations of intertidal sediments	all abundant infauna	2 days	63	OSO	3.7	500

1. Twelve of the studies (those references not preceeded by an asterisk) included in this table were designed to experimentally test habitat preferences of settling larvae, or juvenile and adult macrofauna and meiofauna recruited into specific sediment treatments (e.g., grain sizes). The remainder of the studies (preceeded by asterisks) compared larval settlement or recruitment into environments whose differences could only be hypothesized: settlement into traps raised above the seabed versus recruitment into bottom sediments (Thorson 1946; VanBlaricom 1978; Santos and Simon 1980a; Bhaud et al. 1981; Hannan 1981), settlement into traps moored in different locations in the water column (Reish 1961), and recruitment into sediments at different locations on the seabed (Muus 1966, 1973). ING = information not given in the paper; NA = not applicable to this study; OSO = one station only was sampled, P = polychaete, B = bivalve

proposed a variety of predictions for the relationships between distributions of functional groups of organisms in dense assemblages and larval settlement phenomena. She argues that patterns result from competitive exclusion resulting in differential settlement of larvae, once dense assemblages have been established, and not from differential post-settlement survival. For each case, Woodin cites literature to support the prediction. Most of these examples are misleading because the studies ususally did not collect the initially settled larval stages of the organisms. For example, the second prediction in Woodin's 1976 paper stated that, because larvae of small burrowing polychaetes can be filtered by suspension feeders, and because the physical barriers made by tube-builders would impede progress in burrowing, the burrowers should reach highest abundances among deposit feeders; the studies of Woodin (1974) and Sanders (1958) are cited to support this prediction. Neither of these studies adequately collected the larval stages of the species considered. Woodin (1974) found increased abundances of the burrowing polychaete, Armandia brevis Moore, in areas void of tube-builders versus areas in dense tube-building assemblages. However, she used a 500-μm screen to sieve the sediments and, therefore, probably did not collect the initially settled larval stages of A. brevis. From 29 to 88 percent of A. brevis settling into defaunated sediment traps raised above the sediment surface (collection intervals ranged from 2 to 33 days) passed through a 500-μm screen to be retained on a 250-μm screen in the study of Hannan (1981) (Hannan, unpublished data). From a laboratory study of

A. brevis development, Hermans (1964) found that fully developed planktonic larvae ready to settle and metamorphose are only 0.1 mm in diameter. Thus, A. brevis could have initially settled among the tube-builders at Woodin's study site, suffering near or complete mortality before growing to a size retained on a 500-μm screen. Likewise, Sanders (1958) used a 500-μm screen in his benthic survey. The high densities of the burrowing polychaete, Nepthys incisa Malmgren, when co-occurring with the burrowing clam, Nucula annulata Hampson (this species was originally called Nucula proxima Say in Sanders [1958] but was described later as N. annulata in Hampson [1971]), than when co-occurring with the tube-building amphipod, Ampelisca spinipes Boeck, may again be the result of differential post-settlement mortality. While newly settled N. incisa are probably retained on a 500-μm screen (Lacalli 1980), newly settled N. annulata would pass through this screen size (J.F. Grassle, personal communication). Thus, the observed patterns may be the result of post-settlement mortality and not of differential habitat selection.

A few novel benthic survey studies (Baggerman 1953; Pratt 1953; Fager 1964; Tyler and Banner 1977) did favor the passive deposition hypothesis to explain patterns of infaunal species distributions. Curiously, the passive deposition hypothesis was suggested to these researchers by the same kinds of correlations between sediment grain sizes and animal distributions that led most other authors (e.g., see reviews by Thorson 1966; Gray 1974) to conclude that larvae actively select for particular sedimentary environments. The opposing interpretations of these patterns of distributions reflect the need

for rigorous experiments to elucidate precisely the mechanisms controlling initial larval settlement in soft-bottom environments.

1.2.5 Pattern and mechanism: A problem of spatial scales

Perhaps the greatest limitation to the data from all studies of habitat selection by larvae is that the spatial scales (millimeters to tens of meters) over which active larval choice has been demonstrated are one to six orders of magnitude smaller than the spatial scales (tens of meters to kilometers) over which patterns of species and sediment distributions are observed in the field (Moore 1975 also discussed this problem). Maximum distances between sediment treatments in laboratory experiments on active habitat selection ranged from 1 mm to 137 cm (Table 1.4); for field habitat selection experiments, maximum distances between treatments ranged from 26 cm to 20 m (Table 1.5). Minimum distances between stations in early subtidal field surveys of infauna and sediment distributions were often defined by the manuverability of the vessel and the accuracy of shipboard-operated navigational equipment. Thus, the minimum distances between stations for shipboard-sampled communities ranged from 50 m to 64 km (Table 1.2), while intertidal communities could be sampled at closer intervals (10 m to 90 m, Table 1.2). The purpose of most benthic surveys was to delimit community composition in relation to sediment type, so large (tens of meters to tens of kilometers) distances between sampling stations also were desirable because significant differences in bulk properties of sediments (e.g., grain size) were easily detected at these spatial scales.

When patterns of community composition and structure were

delimited at smaller spatial scales (e.g., scales on the order of 1 m to 10 m in Jones 1961; of 10 cm to 1 m in Angel and Angel 1967; of 100 cm in Gardefors and Orrhage 1968 and Jumars 1976; of 10 m in Gage and Geekie 1973a; of 10 cm in Olsson and Eriksson 1974; and of 100 cm to 1 m in Grassle et al., 1975), sediment samples were not taken at each infaunal sampling location (except in Angel and Angel 1967). The entire area sampled in these small-scale dispersion studies was usually considered homogeneous in its bulk sediment characteristics, based on one to a few sediment samples from the area. Thus, the spatial patterns and scales of diversity detected in these studies were usually attributed to processes other than those directly related to bulk properties of sediments.

The small-scale patterns of species distributions and diversity detected in the aforementioned studies are the only patterns to which results of habitat selection experiments can be applied directly. Even though bulk properties of sediments were presumed to be constant within the areas sampled in these studies, Angel and Angel (1967) and Jumars (1976) acknowledged that small-scale alterations in sediment characterisitics could exist. It is well-known among sedimentologists that local heterogeneity in sediment topography causes significant small-scale (centimeters to meters) variations in sediment grain size because of changes to the near-bottom flow regime; recently Eckman (1983) demonstrated that patchiness in infaunal distributions at these small scales is directly related to this sediment heterogeneity. In addition, detailed analyses of sediment characteristics using microscopic methods and staining techniques (Whitlatch and Johnson

1974) indicate that bulk sediment analyses obscure variation in sediment properties (e.g., protein, carbohydrate, and lipid contents) to which organisms may respond (Whitlatch 1974, 1980). Many laboratory studies of habitat selection have demonstrated that there are chemical and biological substances (e.g., chemical conditioning of sediments by adults or the abundance and composition of bacterial populations) in sediments which augment grain size as attractive factors to stimulate or enhance larval settlement. Thus, within an area of homogeneous sediment type (based on grain size analysis), larvae may actively select for microhabitats based on these other aspects of sediments.

In summary, larvae may select for microhabitat at small spatial scales (millimeters to tens of centimeters) based on sediment characterisitics other than just grain size (determined from bulk sediment analyses). The capability of larvae to distinguish between and actively select for habitats with distinctly different grain sizes and separated by large distances is yet to be demonstrated. The passive deposition hypothesis may resolve this problem because this hypothesis states that larvae are deposited at the same spatial scales applying to sediment transport and deposition. At this time, passive deposition of larvae represents the simplest and most feasible mechanism for creating initial distributions of larvae in the field.

1.2.6 Tests of the passive deposition hypothesis

The passive deposition hypothesis must be tested experimentally. The ambiguities in data interpretation, discussed above, can only be resolved by detailed experiments. Provided below

is a brief review of the experiments, to date, on relationships between hydrodynamical processes and larval settlement phenomena (Baggerman 1953; Eckman 1979, 1983; Hogue and Miller 1981). The work of Baggerman (1953) indicates that the passive deposition hypothesis is a feasible alternative explanation for distributions of cockle spat. By quantifying the effects of certain hydrodynamical processes on the seabed, Eckman's (1979, 1983) studies provide more direct experimental evidence that small-scale ($\leq$ centimeters) patterns of infaunal recruitment are either due to passive deposition of organisms or to active selection by organisms for features of particular hydrodynamical regimes (i.e., low flow areas where detritus may accumulate). Similar experimental work by Hogue and Miller (1981) supports Eckman's conclusions. However, passive deposition of larvae, in the field, over the spatial scales that sediments are deposited ($\leq$ tens of meters) remains to be experimentally demonstrated.

Baggerman (1953) determined that a range in sizes of cockle spat were likely to be transported and deposited like fine sediments by showing that the passive sinking rates (measured in the laboratory) of spat were similar to the passive sinking rates of the sediments transported at the study sites. In addition, he tested the passive deposition hypothesis experimentally by manipulating the near-bottom flow regime in the field. Baggerman placed on the seabed vertical barriers (screens) in specific orientations (evidently to be perpendicular or parallel to the flow) and sampled for cockle spat near and away from the screens. Collections of spat were significantly greater near the screens than away from them. These results

supported Baggerman's prediction that more passively settling spat would be deposited in regions of relatively slower flows, formed by "the current shadow [boundary layer of fluid] near the screens" than in the faster flows away from the screens. The distribution of cockle spat in the field was also significantly greater in topographic lows, where fine sediments accumulate due to lower bottom shear stress, compared with topographic highs. However, Baggerman did not experimentally eliminate the alternative hypothesis that larvae could actively select for settlement sites in fine sediment depositional areas due to an increased detrital food source which may also accumulate in these low flow regions.

Eckman's (1979, 1983) laboratory flume and field experiments provide direct evidence that patterns of larval, juvenile and adult recruitment at very small spatial scales (millimeters to centimeters) are determined, at least in part, by the nature of near-bottom flows. In the first study (Eckman 1979), worm tubes were simulated by small sewing needles (< 1-mm diameter) inserted, at regular intervals, into defaunated field sediments. By natural erosion, the needles protruded a few millimeters above the seabed. From contiguous core samples across the experimental area, Eckman found that one of the dominant small-scale dispersion patterns for two infaunal organisms correlated precisely with the needle spacing. Hogue and Miller (1981) repeated Eckman's needle experiments and found that nematode dispersion patterns were also correlated with the needle spacing. Eckman (1979) hypothesized, a posteriori, that local changes in patterns of flow at the sediment/water interface result in

shear stress patterns which cause passive collection of detritus or organisms in the lee of the needles. The organisms may be passively deposited in the lower stress region downstream of the needle and/or the organisms may actively choose this region for feeding because it passively collects or prevents the scouring of detritus. Eckman argued that his hydrodynamic hypothesis was plausible because the influence of the needles on the flow represented a spatial distance (< 5 mm) consistent with the scale of increased abundances of organisms. He further suggested that alternative hypotheses regarding biological interactions are improbable because these interactions would occur on larger scales.

In the second study (Eckman 1983), 6-mm diameter plastic straws (simulating stalks of marsh grass) were inserted into sediments in three densities. The numerical density of the stalks changes the rate of fluid transport near the bed and the bottom shear stress. The magnitudes of these hydrodynamical effects were determined in laboratory flume experiments enabling a priori predictions of hydrodynamical effects on infaunal recruitment in the field. Thus, Eckman hypothesized that there would be a relative increase in the supply rate of organisms to an area for density treatments with higher fluid transport rates and that deposition or retention of organisms on the seabed would be relatively higher for density treatments with lower values of boundary shear stress. In field experiments using the three densities of simulated marsh grass in defaunated sediments, the patterns and rates of recruitment of several infaunal taxa supported the a priori predictions,

indicating that organisms respond to changes in flow processes over very small spatial scales.

1.2.7 Summary of literature review

In summary, many benthic survey studies have shown that patterns of infaunal species distributions correlate with sediment grain size. Larvae may actively select these sediments during the settlement process or larvae may be passively reach the seafloor where particular sediments (with fall velocities similar to larvae) initially settle. Most studies did not experimentally distinguish between these alternative hypotheses. The active habitat selection hypothesis was generally favored because laboratory choice experiments showed that larvae preferentially settled in certain sediment treatments. However, laboratory experiments were conducted on spatial scales one to three orders of magnitude smaller than the patterns of species distributions observed in the field. Even field experiments on habitat selection by larvae were conducted at spatial scales smaller than the scales of patterns requiring explanation. Field tests of the passive deposition hypothesis have indicated that recruitment of organisms at very small spatial scales (millimeters to centimeters) is, at least in part, determined by the hydrodynamic nature of flows near the seabed. One study (Baggerman 1953) has demonstrated the feasibility of passive larval settlement occurring at the same spatial scales that sediments, with fall velocities similar to larvae, are deposited. However, the literature is void of direct evidence that larvae act like passive particles in near-bottom flows or that larvae settle passively over the spatial scales that

sediments are deposited.

1.3 Significance of the Present Study

The present study is a necessary first step toward testing the passive deposition hypothesis. Unless larvae act like passive particles as they fall toward the seabed in turbulent field flows, they are unlikely to be passively deposited on the bottom. Thus, it is important to first determine, (1) if larvae sink like passive particles in near-bed flows and, (2) what kinds of particles (e.g., particle fall velocities) most accurately predict the distribution of larvae in waters near the seabed. This information then can be used for predicting sites of larval deposition in the field and for designing laboratory flume experiments to directly test the passive deposition hypothesis.

1.3.1 Compatibility of the passive deposition and active habitat selection hypotheses

Passive deposition of and active habitat selection by larvae should not be considered mutually exclusive alternatives. Several biological and physical variables, including the mass density, size, and shape of the organism, the period of time it has already spent in the water column, characteristics of the flow regime and the substrate relief are likely to affect the degree to which an organism is passively deposited. There are a variety of ways (listed below) in which the passive deposition hypothesis would be compatible with the existing data on habitat selection. In addition, these phenomena may not be confined to the larval stages. Evidence is mounting that

post-larvae, adult infauna and meiofauna periodically occur in the water column (Table 1.1). Indirect evidence (extensive sampling of the seabed) also indicates that infauna and meiofuna may actively or passively enter the water column for passive migrations to new locations (Baggerman 1953; Trueman 1971; Dauer and Simon 1975; Farke et al., 1979; Grant 1981; Palmer and Brandt 1981; Hogue 1982). Thus, the data on all organisms (larvae of infauna, postlarvae and adult infauna, and meiofauna) whose life histories may involve water column excursions, is discussed below.

(1) Certain species, morphological types and/or developmental stages of larvae are capable of controlling their position in the water column. Data on swim speeds of planktonic infaunal larvae, other than Crustacea, are sparse (see review by Mileikovsky 1973); swim speeds and other behavioral responses of larval crustaceans are given in Forward (1976), Cronin (1979), Cronin and Forward (1979), Sulkin et al., (1979), Forward and Cronin (1980), Spaargaren (1980), and Schembri (1982). If larvae can also effectively control their position by swimming in waters near the seabed, then certain species may be better able to select settlement sites than species which are weak swimmers or floaters (e.g., see comparative study of swim speeds by Spaargaren 1980).

(2) Developmental constraints may dictate a finite period for active habitat selection in some larvae; after this period larvae would be passively deposited either because they have metamorphosed and are no longer adapted for swimming or because energy reserves required for active habitat selection have dwindled. Certain species

have very well-defined pelagic periods (see reviews by Scheltema 1974, Crisp 1974, and Strathmann 1978) and some larvae metamorphose in the water column prior to settling onto the seabed (Baggerman 1953; Thorson 1966; Pechnik 1980; Lacalli 1980), sometimes in response to environmental cues (Day 1977; Rice 1978). Other species of invertebrate larvae can delay metamorphosis for long periods of time (e.g., Wilson 1958, 1977; Cobb 1968; Birkeland et al., 1971; Day and Blake 1979; Kempf 1981), but will still metamorphose in the laboratory when presented with the appropriate substrate.

(3) Power requirements for a larva to swim depend on the mass density, size, shape, number of cilia and ciliary banding patterns of the individual (see Hutchinson 1967; Holwill 1977; Purcell 1977; Sleigh and Blake 1977; Spaargaren 1980; Vogel 1981 for discussions of physical properties affecting movements of low Reynolds number organisms); thus, the species- or age-specific values of these parameters may also determine the degree to which larvae are passively deposited. There is evidence that mass density (Gross and Raymont 1942; Spaargaren 1979) and size, age, and shape (Ryland and Stebbing 1971; Carriker 1951; Sandifer 1975; Hall et al., 1980; and reviews by Hynes 1970; Waters 1972; Strathmann 1978) of larvae and organisms within the meiofauna size range affect their position in the water column and the way the organisms are transported by currents.

(4) Certain behaviors or responses of organisms may augment passive physical processes to produce observed patterns of species distributions. Once organisms have been passively deposited in an

area, they may actively re-enter some sediments over others (Alldredge and King 1977; Grant 1981; Palmer and Brandt 1981). Organisms also may assist in their own passive transport by actively coming to the sediment surface ("retreating" from sediments) to be subsequently resuspended and transported like surface flocs (Bell and Sherman 1980). Wilson (1948) showed that larvae of the polychaete, Ophelia bicornis Savigny used the current to help them detach from undesirable sediments and move downstream. Active retreat has been linked to food limitation (Grant 1980), presence of an infaunal competitor (Wilson 1983), and tidal height (Trueman 1971).

(5) Some flow regimes may permit effective habitat selection by larvae, while other flow regimes may sort and passively deposit all seston. By simultaneously sampling of the water column and the seabed or intensively sampling the seabed, recent studies (Hagerman and Rieger 1981; Hogue 1982; Dobbs and Vozarik 1983) indicate that storms are effective in resuspending and transporting a variety of infauna and meiofauna. When flow conditions are more benign, these organisms do not occur in the water above the seabed. In addition, the studies of Bell and Sherman (1980) and Plamer and Brandt (1981) suggest that meiofauna are resuspended and transported only during certain phases of the tide. Other support that current velocity may determine the degree to which organisms can actively relocate on the seabed comes from observations of rheotaxis of permanent meiofauna (Boaden 1963, 1968; Gray 1966b), soft-bottom invertebrate larvae (Stancyk 1973; Lucas 1975), demersal zooplankton (Emery 1968; Alldredge and King 1977) and drifitng stream insects (see reviews by

Hynes 1970; Waters 1972).

(6) Small-scale bottom topography (bottom roughness elements such as biological bedforms or ripples) and characteristics of the local benthic boundary layer may determine where larvae are passively deposited. While Eckman (1979, 1983) and Hogue and Miller (1981) provide direct evidence of this, several studies provide indirect evidence because larval, postlarval or adult infaunal organisms accumulated in depressions on the bottom (Baggerman 1953; Pratt 1953; Pamatmat 1968; Sameoto 1969b; Howard and Dorjes 1972; Farke et al., 1979; McLusky et al., 1983) or in seagrass beds that baffle water motion (Orth 1977; Scheibling 1980). As previously noted, an alternative explanation for such accumulations is that organisms preferentially select for or survive in these areas because they collect detritus.

(7) The timing of local physical processes with the local availability of larvae competent to settle may also determine when and where deposition occurs. For example, Fager (1964) hypothesized that a rip current containing larvae ready to settle produced a unique and extensive patch of worms running in an elliptical pattern parallel to shore.

1.3.2 Applied aspects to this research

Identifying when and where a particular mechanism (e.g., passive deposition or active habitat selection) is likely to produce the patterns of larval or adult species distributions sampled in the field is a basic and largely unresolved problem in benthic marine ecology today. Knowledge of these mechanisms is also vital for many

applied problems, including designing benthic monitoring programs, making policy decisions regarding human disturbance activities (e.g., waste disposal, drilling for oil, dredging, and submarine construction) in the oceans and in situ culturing of marine invertebrates for food.

The following two examples are given to illustrate how knowledge that a particular mechanism controls larval settlement implies a specific prediction or action concerning an applied research problem. The first example involves the deposition of drilling muds and cuttings onto sediments during oil drilling activities. The principle components in drilling muds are barite (barium sulfate) and bentonite (clay) which together constitute 79.1 to 99.9 percent of the muds by weight (e.g., see Danenberger 1983). These drilling muds are presently considered to be chemically unreactive because the most abundant chemical in the muds is barite (drilling muds used on Georges Bank were 43 to 71 percent barite by weight [Danenberger 1983]) is unreactive and bentonite, the second most abundant component of the muds (21 to 49 percent for drilling muds on Georges Bank [Danenberger 1983]) is natural clay. The physical characteristics of the drilling muds distinguish them from natural quartz sediments. The drilling muds are in the silt and clay size range (< 63 μm) of naturally occurring sediments, but are considerably more dense than quartz particles (mass density = 4.50 g/cm^3 for barite and mass density = 2.65 g/cm^3 for quartz). Theoretically, the bottom shear stress required to initiate motion of drilling muds would be approximately twice the stress for initiating motion of the same sizes

of quartz particles (Butman and Moody 1983). Thus, it is reasonable that in certain flow regimes drilling muds would remain on the seabed where similarly sized quartz particles would be eroded and transported away. Naturally occurring sediments at such locations would be characteristically larger than the drilling muds.

Predictions of the effects of these drilling muds on the natural benthic infaunal assemblages at the drill site differ radically depending on the mechanism controlling patterns of initial larval settlement. At the drill site, if larvae choose where to settle by selecting for particular surface sediment grain sizes or some aspect of sediments related to grain size (e.g., water content, cohesiveness, or microbial population density), then the drilling mud veneer may alter the species composition in the affected area. That is, prior to drilling mud deposition, larvae preferring a coarser-grained sediment would select this area of the seabed, while drilling mud deposits would attract species preferring finer sediments. If drilling muds were confined only to the very surface sediments, nonsurficial burrowing and tube-building forms may be avoiding sediments where they could actually survive. Likewise, some of these subsurface-dwelling organisms may select the "wrong" environment for settlement, by basing their choice on the surface texture of the sediments, and experience large post-settlement mortality once they burrow below the sediment surface. Thus, it is even conceivable that the affected area would become defaunated because surface sediments attracted the "wrong" species, even though the site is compatible with infaunal life. If larvae are passively

deposited at the drill site, according to local hydrodynamical processes and the physical characterisitics of the larvae, then patterns of initial larval settlement would remain unchanged in affected areas, as long as the drilling mud deposits did not significantly alter the near-bottom flow regime.

In this example, a change in the benthic community is predicted if larvae select for settlement sites based on sediment grain size whereas no change is predicted if larvae settle onto the seabed like passive particles. In addition to knowledge of the mechanism(s) determining initial patterns of larval settlement at the drill site, accurate predictions of the effects of drilling muds on benthic infaunal communities requires at least the following information: (1) characteristics of surface and subsurface sediments prior to drilling, (2) thickness and spatial extent of drilling mud deposits, (3) characteristics and variability of the near-bottom flow regime, (4) availability of larvae for settlement (e.g., knowledge of source populations and the variability in planktonic larval abundances), and (5) life history characteristics of dominant infaunal organisms at the drill site.

The second example of how information on mechanism(s) controlling larval settlement can be used for an applied problem concerns in situ culturing of commercially important invertebrate food items (e.g., scallops, oysters, quahogs, shrimp, crabs, and lobsters). Most of these species have planktonic larval stages; the spatial variability in settlement of these larvae and thus, of adult populations, means that locations of large harvests vary continually.

Clearly, the economic gain from commercial harvests decreases with the amount of searching time required to obtain large numbers of organisms. Thus, if larval settlement can be regularly enhanced at certain locations by artifically altering characterisitics of the seafloor or of the flow regime, the cost per unit effort for obtaining consistently good yields, will decrease. I call this "in situ culturing" of marine organisms.

The specific manipulation required to enhance larval settlement in a particular location depends on the mechanism controlling initial settlement of larvae onto the seabed. If larvae are passively deposited in the field, then artifically creating regions of relatively low shear stress near the seabed would enhance larval deposition. The extent to which flows must be altered depends on the fall velocities of the larvae. Baggerman (1953) has successfully used this technique by erecting vertical barriers to slow down flows next to the seabed; settlement of cockle spat increased near these barriers. For larvae that actively select habitats in the field, enhanced settlement would result only if field sediments were altered so they contained the factors attractive to larvae. This kind of manipulation is difficult to do directly, but could be accomplished by placing trays of attractive sediments on or above the seabed. Again, other information on biological processes (e.g., the presence of predators or competitors in sediments that effect post-settlement mortality) and physical processes (e.g., the variability of local near-bottom flow regimes) is required, in addition to knowledge to larval settlement mechanisms, for success with the aforementioned manipulations.

2. COLLECTION OF PARTICULATES BY NEAR-BOTTOM TRAPS: THEORETICAL ANALYSIS OF THE HYDRODYNAMICAL PROCESSES

2.1 Introduction

The experimental design for testing the biological hypothesis central to this thesis requires trap designs with significantly different particle collection efficiencies, relative to each other. The theoretical analysis, presented here, was a necessary first step toward selecting these trap designs. Although several calibration studies (listed below) have already been performed for a variety of trap designs, the relevance of these studies to the trapping of particles, that are hydrodynamically similar to larvae, in turbulent near-bottom flows was initially unclear. However, once the physical processes that most likely control trapping of this class of particles have been determined, then data from the existing calibration studies can be evaluated in view of the biological hypothesis to be tested here. Trap designs that are most likely to demonstrate the desired biased trapping effects then can be selected for tests in a laboratory flume (see Chapter Three). In addition, the flume experiments can be appropriately designed in view of the hydrodynamical principles of particle trapping.

2.1.1 The use of traps to monitor particulate flux

Particle-collecting traps are presently a popular research tool for estimating the quality and quantity of material falling out of oceanic and limnologic water masses (see reviews of Bloesch and Burns 1980; Blomqvist and Hakanson 1981; and the annotated bibliography of

Reynolds et al., 1980). Concern regarding possible biased sampling by traps eventually motivated studies on the accuracy and precision of various trap designs. Most of these studies (over 40 listed in Reynolds et al., 1980) involved comparisons, in the field, of particle collections either by several trap designs or by a trap and some other measure of particulate flux (e.g., Pb^{210} flux in traps compared with Pb^{210} flux from the atmosphere, Knauer et al., 1979). Because no unbiased value for the "true" flux of particles in the field is available, these studies furnish only comparative data and estimates of trap precision (in the few cases where replicates were deployed), but not estimates of trap accuracy.

Trap calibrations for accuracy estimates are possible in laboratory flows as long as all parameters dynamically important to the processes of particle trapping are controlled; dynamic- and geometric-similarity to field conditions also must be maintained. The handful of such quantitative calibration studies to date (Hopkins 1950; Davis 1967; Peck 1972; Tauber 1974; Gardner 1977, 1980a; Hargrave and Burns 1979; Lau 1979; Welton and Ladle 1979) have provided valuable information on particle trapping for some specific trap designs, flow conditions and particle types. However, quantitative trap calibrations for the bulk of realistic field flows have not yet been performed (see Section 2.3.1). Even so, results of calibration studies often have been extrapolated far beyond the range of hydrodynamic conditions actually tested. Recently, these extrapolations, coupled with the vast amount of information on field-tested traps, have been developed into general criteria for

design, construction, and deployment of unbiased trap samplers (see Bloesch and Burns 1980; Reynolds et al., 1980; Blomqvist and Hakanson 1981). However, because traps have been calibrated only for a narrow range of field flows and particle types, flux estimates even from traps which meet the general criteria specified in these review papers should be viewed with caution. Suggesting that any particular trap design will unbiasly estimate particulate fluxes in a wide range of environments is premature.

This theoretical analysis was motivated by the fact that particulate fluxes are routinely and uncritically estimated using traps in a wide range of flow fields for which the traps were neither experimentally calibrated nor theoretically evaluated. Undoubtedly, more laboratory calibration experiments are needed. A priori knowledge of the dominant hydrodynamical processes controlling particle trapping indicates the physical parameters that must be carefully monitored and the physical variables that must be carefully controlled during calibration experiments. In addition, a series of trap tests dictated by specific a priori hypotheses of biased trapping effects is the most efficient experimental procedure for determining the relative importance of several parameters to a particular physical process.

2.1.2 Previous theoretical analyses of particle trapping

Given the plethora of studies which attempted to determine sediment trap collection efficiencies either by calibration in the laboratory or by comparisons in the field (see annotated bibliography of Reynolds et al., 1980), it is surprising that only two papers

(Hargrave and Burns 1979; Bloesch and Burns 1980) provide formal theoretical treatments of the hydrodynamical processes governing particle collection by traps. (Emery's (1978) theoretical expression for quantifying resuspended material in lakes specified a particular trap design, but did not address the general problem of accurately collecting falling material in traps; thus, this study will not be considered further.) Many of the calibration or comparison studies do offer hypotheses, based on some fluid dynamic principles, regarding the nature of particulate trapping. However, because these discussions are not embedded in a theoretical framework, the resulting predictions are often ambiguous or conflicting.

Predictions regarding collections by the "Tauber" trap (a cylinder covered by a convex collar which reduces the mouth diameter to about half the body diameter, see diagram in Figure 2.2) exemplify some of the existing confusion in the literature. Tauber (1974) suggested that, compared to other pollen traps, this trap design would collect different-sized particles at much more similar efficiencies in turbulent flows. The collar surrounding the trap mouth would insure a smooth flow of fluid over the trap so that no "vortices" would be shed into the trap mouth. Gardner (1977) argued that a Tauber-like trap should overcollect particles in both still water and moving fluid because particles fall out of the water mass directly underneath the overhanging wall surrounding the trap mouth before new particles are able to enter this area. The water under the wall becomes relatively less dense than the surrounding water; the low-density water rises out of the trap and is replaced by water with

a greater particle concentration so the trap over collects particles. Reynolds (1979) predicted that Tauber traps would tend to "exaggerate the settling rate" of particles from flows with low turbulence, but undercollect particles at higher turbulence levels. All authors claim some theoretical, and for Tauber (1974) and Gardner (1977), direct observational (dye studies) basis for their predictions; however, each addresses only a particular (and not necessarily the same) dynamical process contributing to a certain trapping behavior. In fact, the experimental results of calibrating (Tauber 1974; Gardner 1977, 1980a) and comparing (Reynolds 1979) the Tauber trap show that it acts as both an overcollector and an undercollector depending on the particles and the flow velocity used in experiments and on the criteria for evaluating collection efficiency.

A unified model based on a careful analysis of all hydrodynamical processes important to particle trapping would help resolve the apparent ambiguities in predicting and interpreting results of particle trapping experiments. Conflicting results of trapping experiments in different studies may become more consistent when each study is appropriately placed along a hydrodynamic continuum and evaluated in light of the model predictions for that particular range of conditions.

Both of the previous theoretical analyses of particle trapping (the studies of Hargrave and Burns [1979] and Bloesch and Burns [1980]) did not consider the characteristics or the behavior of particles moving in the flow; these studies analyzed only the nature of trap collections within the flow field. In addition, the scope of the

theoretical analyses in these studies was limited. Hargrave and Burns (1979) determined the relative importance (using dimensional analysis) of the variables involved in only one aspect of particle trapping, resuspension of particles inside a trap. Bloesch and Burns (1980) described the general process of particle trapping using a control volume analysis (i.e., by balancing the mass entering and leaving a trap). They discussed how various terms in this mass balance would be effected if the trap mouth area (A_m) did not equal the trap base area (A_b). However, they did not proceed to theoretically evaluate the effects of other relevant parameters and variables on terms in their equation.

2.1.3 The unique nature of this theoretical analysis

The theoretical analysis presented in this chapter provides both a general analysis of the hydrodynamics of particle trapping and an analysis of specific effects. In Section 2.2, the physical variables involved in the process of particle trapping are parameterized using a dimensional analysis. The dimensional analysis identifies the dimensionless parameters most likely to effect particle collection efficiencies of traps, but the analysis does not provide information about the precise quantitative nature of the dependence between the parameters and collection efficiency. Thus, in Section 2.3, results of the published laboratory flume studies that determined particle collection efficiencies of various traps designs are evaluated relative to the dimensionless parameters. This summary of the published results helps to elucidate the direction of the dependence (e.g., positive or negative correlations) between each parameter and

particle collection efficiency. Then, in Section 2.4, specific physical models are developed to account for these relationships. These theoretical models are presented as a series of testable hypotheses regarding the nature of trap biases and serve two purposes. First, the theoretical models and the hypotheses dictate various aspects of the experimental design for future trap studies. Second, the hypotheses suggest which trap designs are likely to display the biased trapping effects required to test the biological hypothesis central to this dissertation. (Several of these designs were then tested in a laboratory flume, see Chapter Three.)

2.2 Dimensional Analysis of the Independent Variables Involved in Particle Trapping

A dimensional analysis of the independent variables involved in particle trapping is a useful way of determining meaningful dimensionless parameters to describe the process and it provides a physical basis for predicting which parameters are most likely to affect particle collection efficiencies. Dimensional analysis alone cannot predict the precise physical effects, only that the results are efficiently described if the data are plotted by the dimensionless parameters. Experimental results will indicate the direction of the changes in collection efficiencies, if any changes occur, relative to the direction of changes in the parameters. Once a relationship between particle collection efficiency and any set of the parameters is demonstrated, then further analyses are required to formulate working hypotheses

regarding the precise physical process(es) that may be involved. Although, in some cases, order-of-magnitude estimates can be made to determine if a hypothesized process can account for the observed quantitative effect, in most cases, experimentation is necessary to determine the magnitude of the hypothesized effects and to distinguish between the effects.

For a straight-sided cylinder on a rigid mooring, the particle trapping rate, P, is a function of nine independent variables. The variables are defined and the basic dimensions (L = length, T = time, M = mass) of each variable are listed below.

P = particle trapping rate (in terms of particle number) or the number of particles trapped per unit area per unit time ($1/L^2T$)
d = particle diameter (L)
ρ_p = particle density (M/L^3)
ρ_f = fluid density (M/L^3)
μ_f = fluid viscosity (M/LT)
u_f = flow speed at the height of the trap mouth (L/T)
g = acceleration due to gravity (L/T^2)
D = trap mouth diameter (L)
H = trap height (L)
N_c = number of particles in the fluid per unit volume ($1/L^3$)

Some limitations and assumptions of this dimensional analysis are discussed below. (1) The effects of trap roughness (i.e., the smoothness of the surfaces of the construction materials) is ignored. While trap roughness may effect the hydrodynamic characteristics of trap-induced flows, laboratory experiments can be designed so that these effects are negligible (e.g., by using traps with smooth surfaces such as tenite butyrate plastic or glass). (2) Turbulence

in the oncoming flow regime is ignored. It is assumed that trap-induced turbulence dominates the flow through the trap so the trap "sees" only the mean-stream velocity of the oncoming flow. Because this analysis also assumes that a well-mixed particle suspension approaches the trap, it is not necessary to stipulate a turbulent oncoming flow regime for the purposes of particle mixing. An analysis of the effects of flow turbulence (e.g., unsteady oscillations) on particle trapping is outside the scope of this study, but merits theoretical and experimental investigation. (3) Trap geometries, other than straight-sided cylinders, are not parameterized here; but note that parameterizations of trap shape would include terms other than just D and H. (4) Traps are assumed to be in a horizontal, steady, uniform flow with no vertical shear. No tilt is allowed in the trap. (5) Edge effects of the flow incident on the trap are ignored.

Three basic dimensions (L, T, and M) describe the nine independent variables, so the variables are arranged in six dimensionless parameters, in addition to a parameterization of P. One set of parameters for the variables is

$$\frac{P}{\frac{(S-1)gd^2}{\nu} N_c} = f\left(\frac{u_f}{\frac{(S-1)gd^2}{\nu}}, \frac{u_f D}{\nu}, \frac{(S-1)gd^2}{\nu}, S, N_c d^3 \frac{H}{D}\right) \tag{2.1}$$

where $\rho_p/\rho_f = S$ and $\mu_f/\rho_f = \nu$. The grouping $(S-1)gd^2/\nu$ is the nominal fall velocity of the particle (W) so eq. 2.1 can be further simplified as

$$\frac{P}{WN_c} = f\left(\frac{u_f}{W}, \frac{u_f D}{\nu}, \frac{Wd}{\nu}, S, N_c d^3, \frac{H}{D}\right). \tag{2.2}$$

The left-hand side of this expression is the nominal collection efficiency (E), $u_f D/\nu$ is the trap Reynolds number (R_t) and Wd/ν is the particle Reynolds number (R_p). (Note that for noncylindrical traps, E is also a function of trap geometry.)

Under certain conditions, the right hand side of eq. 2.2 can be considered independent of each of the six dimensionless parameters. For small relative particle concentrations, $N_c d^3 << 1$, such that particles move in the flow and settle independently, then the function is independent of N_c and, thus, of $N_c d^3$. If particle inertia is negligible, such that particle motions are determined only by the flow velocity and the particle fall velocity, then the function is independent of both S and R_p. If the overall flow field has a sufficiently high Reynolds number, then the large-scale features of the flow are independent of R_t so the function may also be independent of R_t. For a cylinder of sufficient height, such that resuspension is negligible, the function is independent of H/D. Finally, for sufficiently large values of u_f/W, the function can be considered independent of this velocity ratio because trap collections may be dominated entirely by flow-induced flushing of the trap interior.

Only the variables composing three of the six dimensionless parameters were routinely measured in laboratory experiments of trapping characteristics; these parameters are $u_f D/\nu$ (or R_t), u_f/W (the dimensionless velocity ratio of particle motion relative to fluid motion), and H/D, (or aspect ratio). Thus, in the next section (Section 2.3), the data from the published laboratory studies

are organized according to these three dimensionless ratios. In addition, the effects of trap geometry on particle collection efficiencies are evaluated. The precise effects of the other three parameters in eq. 2.2 ($N_c d^3$, Wd/ν, and S) cannot be evaluated from experimental observations, but theoretical models suggesting biased trapping mechanisms that involve these terms are provided in Section 2.4. For example, if $N_c d^3$ is not much, much less than one, then individual particles may interact and aggregate in the flow; aggregation would effect W and, thus, any trapping process that is fall-velocity dependent would also be dependent on $N_c d^3$ (if $N_c d^3$ was not $<< 1$).

2.3 Observations from the Literature

Results of the published laboratory studies on particle collection efficiencies of traps in moving fluid (Peck 1972; Tauber 1974; Gardner 1980a; Hargrave and Burns 1979; Lau 1979) are evaluated here, in light of the dimensional analysis (Section 2.2). Some laboratory studies of traps are not included here because they did not involve moving fluid (Hopkins 1950; Davis 1967), because only descriptive, but not quantitative, data are presented in the paper (Anderson 1977; Antsyferov et al., 1977; Honjo et al., 1980; Soutar et al., 1977), or because the trap was not designed for collecting falling particulates in lake or marine systems (Welton and Ladle 1979). Of the remaining studies, two (Peck 1972; Tauber 1974) examined only one trap design (The "Tauber" trap, described in Section 2.1.2 and diagramed in Figure 2.2) collecting pollen, two

(Gardner 1980a; Hargrave and Burns 1979) examined a variety of trap designs collecting natural sediments, and one (Lau 1979) examined the flow of water through cylinders but did not determine particle collections by the traps. The ranges in values of the three dimensionless parameters, R_t, u_f/W, and H/D, and the trap geometries tested in these five published studies and in the present study (see Chapter Three) are given in Table 2.1.

2.3.1 Particle collection efficiency and trap Reynolds number

One requirement for dynamic similarity between laboratory and field flows is that similarity between the laboratory R_t and the field R_t must be maintained (see Section 3.1.2). Particle collection efficiencies of traps were determined for R_t ranging from $4x10^2$ to $5x10^3$ for studies involving natural ocean sediments (Gardner 1980a; Hargrave and Burns 1979) and ranging from $9.9x10^3$ to $9.9x10^4$ for studies involving pollen grains (Peck 1972; Tauber 1974) (Figure 2.1 and Table 2.1). For R_t ranging from $2x10^3$ to $3x10^4$, Lau (1979) measured the residence time of neutrally buoyant oil droplets in traps.

To demonstrate how the relatively narrow range in R_t (of less than an order of magnitude) for sediment traps tested in the laboratory relates to the R_t of traps deployed in the field, plotted in Figure 2.1 are the flow speeds associated with R_t ranging from 10^2 to 10^6, for lines of constant trap diameter. For a R_t of $5x10^3$ (the upper limit for sediment traps calibrated in the laboratory), a 5-cm diameter trap would be calibrated for an 11-cm/sec flow, but a 25-cm diameter trap would be calibrated only

TABLE 2.1

Ranges of Values for the Dimensionless Ratios, R_t, u_f/W and H/D, and Trap Geometries Tested in Six Laboratory Studies

Laboratory study	Approximate[1] range in R_t	Approximate[2] range in u_f/W	Range in H/D for cylinders	Trap geometries tested
Peck (1972)	2.2×10^4 - 4.3×10^4	9.7×10^3 - 1.9×10^4	NCT[3]	Tauber trap (a "short" and a "tall" version, see Section 2.3.3)
Tauber (1974)	9.9×10^3 - 9.9×10^4	4.1×10^3 - 4.1×10^4	NCT[3]	Tauber trap
Gardner (1977, 1980a)	4.0×10^2 - 5.1×10^3	$\geq$ 77	1.0-2.3	Cylinders, funnel traps, baffled funnel traps, small-mouth wide-body traps, segmented basin, flat plate, horizontal tube with silt
Hargrave and Burns (1979)	9.5×10^2 - 4.9×10^3	$\geq$ 2.9	1.2-20.4	Cylinders, baffled cylinders, funnel trap, small-mouth wide-body trap, covered cylinder, tray, trap with horizontal-facing aperture
Lau (1979)	2.3×10^3 - 3.8×10^4	NA[4]	4.7-10.0	Cylinders
Present study (see Chapt. Three)	2.2×10^3 - 1.9×10^4	3.0×10^1 - 7.4×10^2	1.0-3.6	Cylinders, baffled cylinders, funnel traps, plate trap, small-mouth wide-body traps

1. R_t were calculated as described in the caption to Figure 2.1.
2. Values of u_f/W were difficult to estimate because none of the studies, except the present study (see Chapter Three) provided estimates of W for the particles used during trapping experiments. Values of W used in the estimates of u_f/W provided here are given and discussed in Section 2.3.2. For the present study, u_f/W was calculated for W ranging from 0.014 to 0.33 cm/sec (see Figure 3.16) and for u_f = 10 cm/sec (see Section 3.3.3).
3. NCT = no cylinders were tested
4. NA = not applicable; Lau (1979) studied only water motion inside traps, not particle collection characteristics of traps.

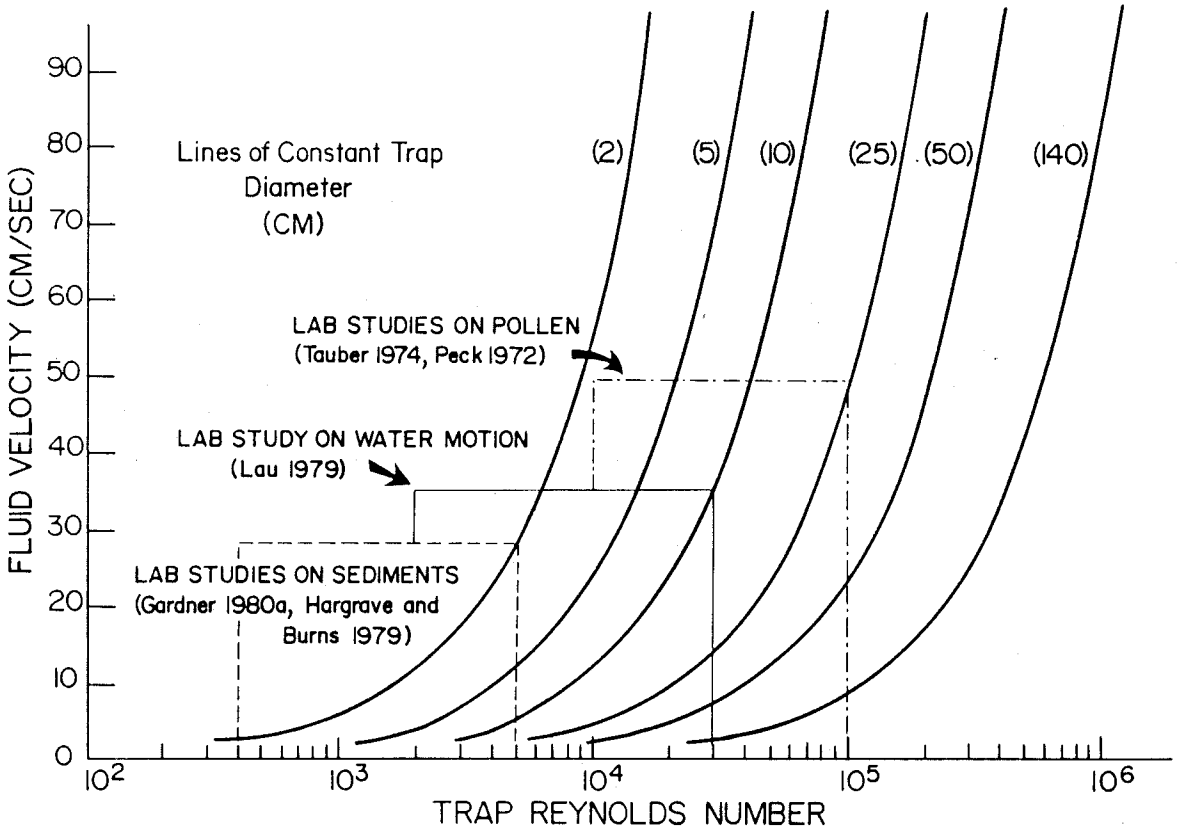


Figure 2.1: Relationship between flow speed and trap Reynolds number for lines of constant trap diameter, showing the range in R_t of traps calibrated in the laboratory. Trap Reynolds numbers were calculated for the studies of Peck (1972), Tauber (1974), Gardner (1980a) and Hargrave and Burns (1979) based on the range of flow speeds and the range of outside mouth diameters of all traps with circular mouth openings, in each study. Because none of these studies provided information on fluid temperatures, water salinities, or fluid viscosities during trap tests, it was assumed that all studies were conducted at a room temperature of 20°C, for the R_t calculations made here. Kinematic viscosities used in R_t calculations were $\nu = 1.185 \times 10^{-2}$ cm^2/sec (30 ppt seawater) for the studies of Gardner (1980a) and Hargrave and Burns (1979), $\nu = 1.01 \times 10^{-2}$ cm^2/sec (freshwater) for the study of Peck (1972), and $\nu = 1.51 \times 10^{-1}$ cm^2/sec (air) for the study of Tauber (1974). The range of Lau's (1979) calculated R_t for the traps that he tested are also plotted in this figure; note, however, that Lau did not give the exact values for L, V and ν that went into each R_t calculation. Thus, it is possible that Lau's (1979) R_t are not strictly comparable to the other R_t calculated here.

for a flow speed of about 2 cm/sec. In coastal ocean environments, water velocities from 0 to 50 cm/sec are common (e.g., Butman et al., 1979; Butman et al., 1982); in some places, such as Georges Bank, MA, tidal currents reach 100 cm/sec for near-bottom flows (Moody et al., in press) and even in deep water (~ 4700 m), flows up to 73 cm/sec have been measured (Hollister and Heezen 1972; Tucholke et al., 1979).

Few field studies using sediment traps have included measurements of flow velocities at or near the trap deployment site and no published study to date has actually measured the fluid velocity at exactly the height of the trap mouth during the course of trap collections; thus, it is impossible to make accurate calculations of trap Reynolds numbers in the field. In addition, field flows are not steady, so the R_t varies over a range of values during a single deployment. However, from the data available (Table 2.2), it is clear that the range of trap Reynolds numbers for field sites exceeds the range tested for sediments in the laboratory by at least an order of magnitude. Sediment traps have been calibrated in the laboratory only for the slowest flows occurring in the field.

The effect of R_t on particle collection efficiency is evident from the study of Tauber (1974). He tested one trap design (the Tauber trap, diagramed in Figure 2.2), collecting pollen in a wind-tunnel, for flow speeds from 100 to 1000 cm/sec. Over this order of magnitude increase in R_t, "collection efficiency" decreased also by an order of magnitude (Figure 2.2) for Fagus sylvatica spores. For the other two spores tested, efficiency decreased by a factor or three or four, for the order of magnitude

TABLE 2.2

Calculated Trap Reynolds Numbers for Sediment Traps Deployed in the Field

Reference	Study Site (depth in meters)	Trap depth (meters)	Depth of velocity measurements (meters)	Outside trap diameter at mouth (cm)	Measured flow speed (cm/sec)	Calculated[1] R_t
Hargrave and Burns (1979)	St. Margaret's Bay, Nova Scotia (13)	10	not measured during trap collections[2]	2.5-21.3	$\leq$ 8	$\leq 1.3 \times 10^4$
Rowe and Gardner (1979)	North Atlantic (2192)	2156-2162	not measured during trap collections[3]	25	$\leq$ 5	$\leq 9.3 \times 10^3$
	(2815)	2316-2803		25	$\leq$ 30	$\leq 5.6 \times 10^4$
	(3577)	3059-3459		25	$\leq$ 30	$\leq 5.6 \times 10^4$
Gardner (1980a)	Woods Hole, MA (6.6)	3.3	3.3	3.9-25.1	$\leq$ 3	$\leq 5.6 \times 10^3$
	(18)	6, 6.9	6, 6.9	3.9-25.1	$\leq$ 21	$\leq 3.9 \times 10^4$
	(12)	6.6	6.6	3.9-25.1	$\leq$ 50	$\leq 9.3 \times 10^4$
Dymond et al. (1981)	Santa Barbara Basin, CA (580)	213-318[4]	330	25-57[4]	0.8-17.5	1.5×10^3 - 7.4×10^4
Lorenzen et al. (1981)	Puget Sound, WA (110)	50	ING[5]	15	$\leq$ 8	$\leq 8.9 \times 10^3$

TABLE 2.2 (cont. - 2)

Reference	Study Site (depth in meters)	Trap depth (meters)	Depth of velocity measurements	Outside trap diameter at mouth (cm)	Measured flow speed (cm/sec)	Calculated[1] R_t
Staresinic et al. (1982)	Peru upwelling (~ 150)	30	30[6]	40.6	10-28	3.0×10^4 - 8.4×10^4
Parmenter et al. (1983a)	Georges Bank, MA (65)	62	64	32	10-50	2.4×10^4 - 1.2×10^5
Parmenter et al. (1983b)	Lydonia Canyon, MA (250-590)	~ 110	~ 110	6.6-50	mean ≃ 15 SD ≃ 10	2.4×10^3 - 9.3×10^4

1. For all R_t calculations, the value for ν of 1.35×10^{-2} cm^2/sec (10°C, 30 ppt seawater at one atmosphere) was used. Most studies did not give information on water characteristics during trap collections so ν could not be calculated exactly. Using one value of ν for all studies probably introduces an error of no more than a factor of two (e.g., for 30 ppt water at 5°C, $\nu = 1.56 \times 10^{-2}$ cm^2/sec and for 30 ppt water at 20°C, $\nu = 1.05 \times 10^{-2}$ cm^2/sec; ν is considerably more sensitive to changes in temperature than to changes in salinity).
2. Current speeds were inferred by Hargrave and Burns (1979) from the study of Webster et al. (1975).
3. Current speeds were inferred by Rowe and Gardner (1979) from the study of Luyten (1977) for the two deep stations and from their own observations using DSRV ALVIN.
4. For the "Soutar cone traps" and the "Gardner cylinder traps" only.
5. ING = information not given in the study.
6. Current speeds were determined from the trajectories of free-drifting sediment traps deployed for $\leq$ 12 hr intervals concurrently with moored sediment traps.

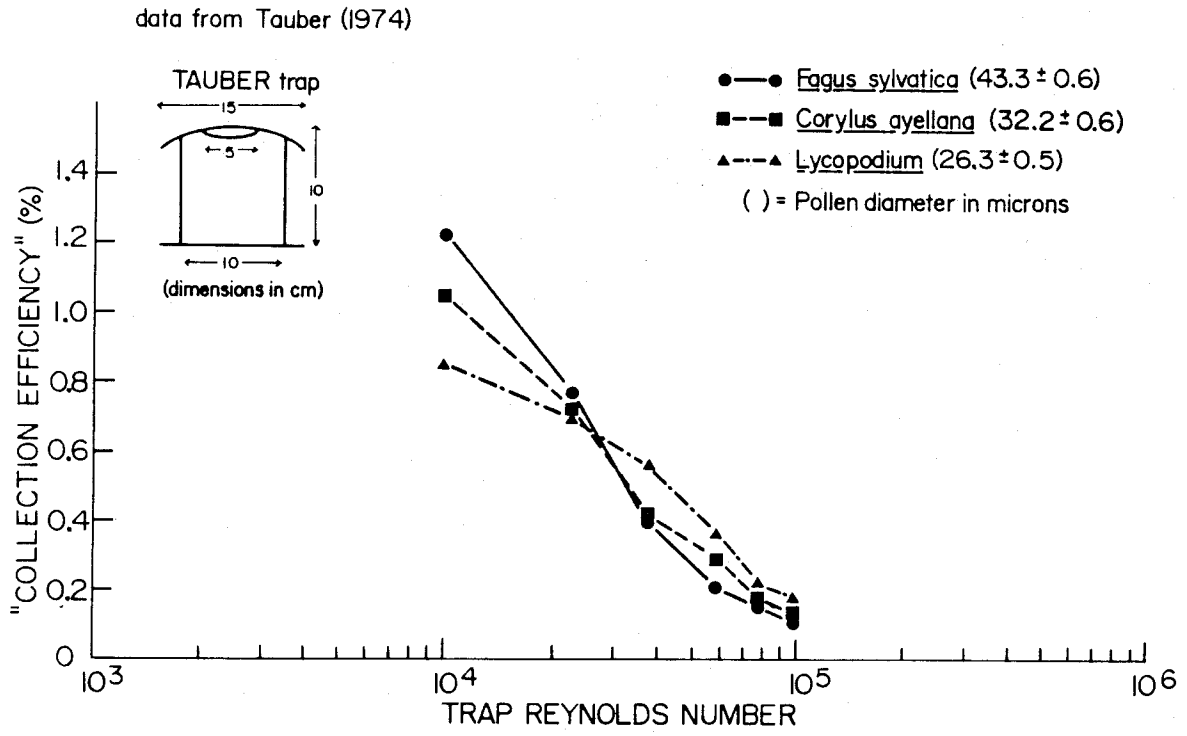


Figure 2.2: Effect of trap Reynolds number on "collection efficiency" in a wind-tunnel study of pollen collectors (Tauber 1974). The Tauber trap (diagramed on this figure) was tested for wind speeds ranging from 100 to 1000 cm/sec. R_t were calculated as described in caption to Figure 2.1. "Collection efficiencies" were the "trap dose" per cm^2 as a percentage of the "area dose" per cm^2. The trap dose is the number of spores collected in a trap divided by the orifice area (19.63 cm^2). The area dose is "the number of spores in cross stripes [on sticky vertical rods placed downstream of the traps] with a total height of 1:0.65 cm divided by the appropriate impaction efficiency [determined experimentally]".

increase in R_t (Figure 2.2). The possibility does exist that the behavior is caused by inertial forces on the particle that clearly are important in air, but not in water (see Appendix I). However, Peck (1972) tested the same trap in water and obtained supporting results.

Peck (1972) tested the Tauber trap at only two flow speeds (14.5 and 28 cm/sec) and different genera of pollen were tested at each speed. However, for pollen $\geq$ 25 μm in diameter "trapping efficiency" decreased by an order of magnitude for an increase in R_t by only a factor of two (Figure 2.3). For pollen < 25 μm in diameter, there was no apparent decrease in efficiency with increasing R_t.

For the two sediment trap studies (Gardner 1980a; Hargrave and Burns 1979), a clear trend of decreasing efficiency with increasing R_t was not apparent. However, sediment trap tests were conducted at a range of R_t about an order of magnitude smaller than the range of R_t during pollen trap tests (compare Figures 2.4 and 2.5 to Figures 2.2 and 2.3). In Gardner's (1980a) study, three cylinder designs and a small-mouth, wide-body trap were tested at flow speeds of 4.4 and 9.5 cm/sec. For each trap design, "trap efficiency" increased slightly (by a factor of 0.7-0.8) with increasing R_t (Figure 2.4). In Hargrave's and Burns' (1979) study, cylinders ranged from 2.5 to 12.8 cm in mouth diameter, but each had a different aspect ratio (this problem is discussed later, see Section 2.4.2); all cylinders were tested at the same flow speed (4 to 5 cm/sec). For traps with aspect ratios $\geq$ 2.6, "percent collection efficiency" decreased very slightly with increasing R_t (Figure 2.5). The error

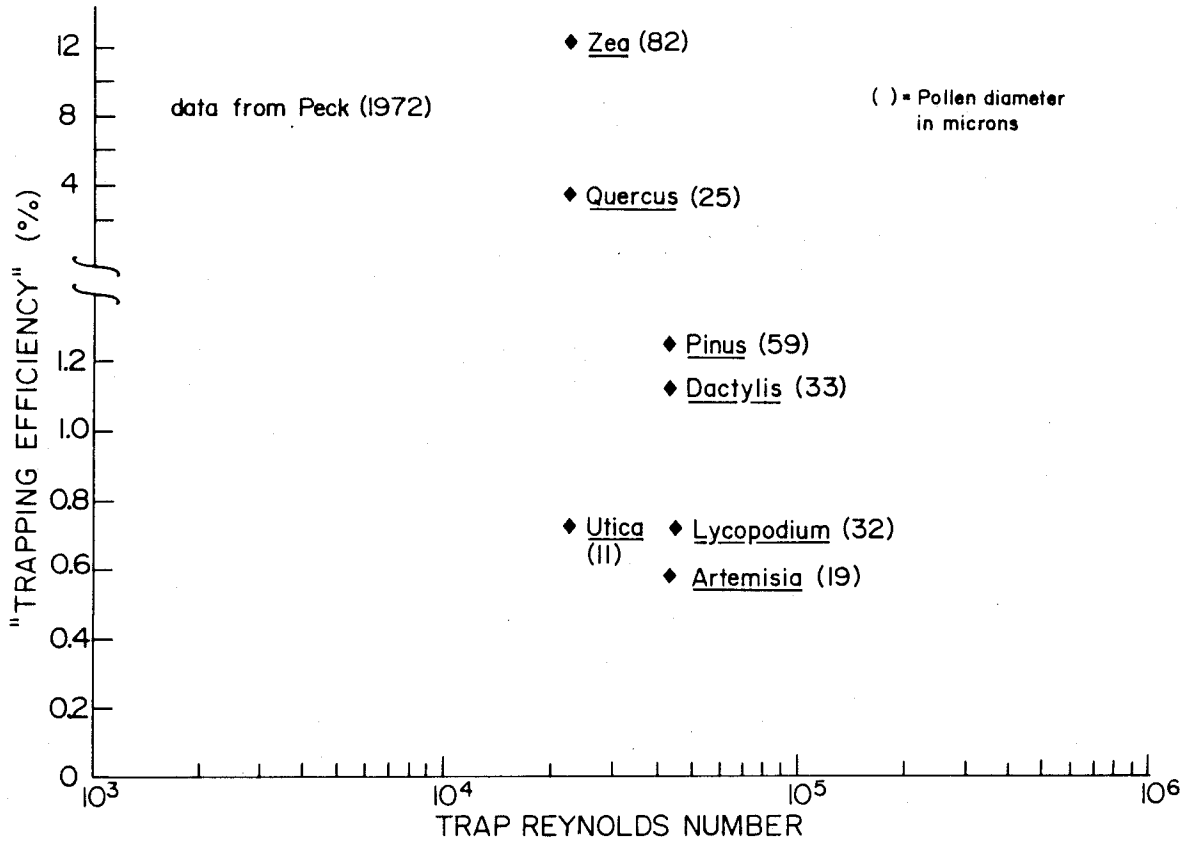


Figure 2.3: Effect of trap Reynolds number on "trapping efficiency" in a freshwater study of pollen collectors (Peck 1972). The Tauber trap (diagramed on Figure 2.2) was tested for flow speeds of 14.5 and 28 cm/sec. R_t were calculated as described in the caption to Figure 2.1. "Trapping efficiencies" were calculated as in the study of Tauber (1974) (see caption to Figure 2.5) except that here "area dose" is $\bar{c}ut$, where $\bar{c}$ = "average concentration per unit volume during experiment," as measured in a large water sample (665 ml) taken from the flume during each experiment, u = "velocity of flow," and t = "total time of experiment (seconds)."

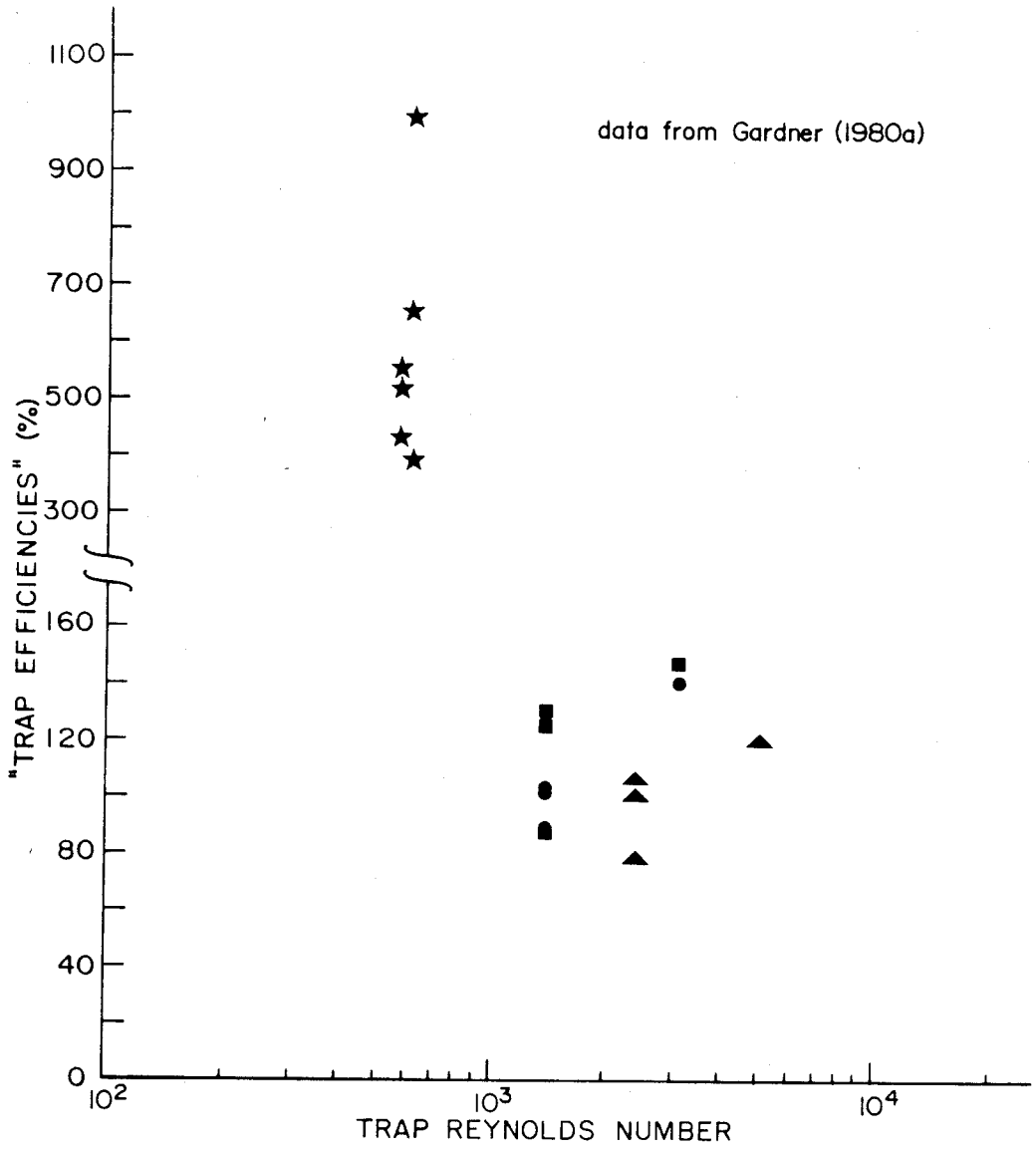


Figure 2.4: Effect of trap Reynolds number on "trap efficiencies" in Gardner's (1980a) seawater study of sediment collectors. Dimensions of the trap designs are given below Figure 2.7; data for his trap design A (triangles), B (squares), C (circles) and L (stars) are plotted here. Note that trap L is not a straight-sided cylinder (see Figure 2.9). Traps were tested at flow speeds of 4.4 and 9.5 cm/sec; other characteristics of these flume experiments are given in Table 4 of Gardner (1980a, page 24). R_t were calculated as described in the caption to Figure 2.1. The flow was seeded with natural sediments < 63 μm in diameter (95 percent of the particles were < 26 μm in diameter). "Trap efficiencies" were calculated as the "flux measured by the trap[s] (mass/cm^2/time)" as a percentage of the "sedimentation rate on the flume bed (mass/cm^2/time)." The sedimentation rate was calculated as the difference between the concentration of suspended particles at the beginning and at the end of each experiment.

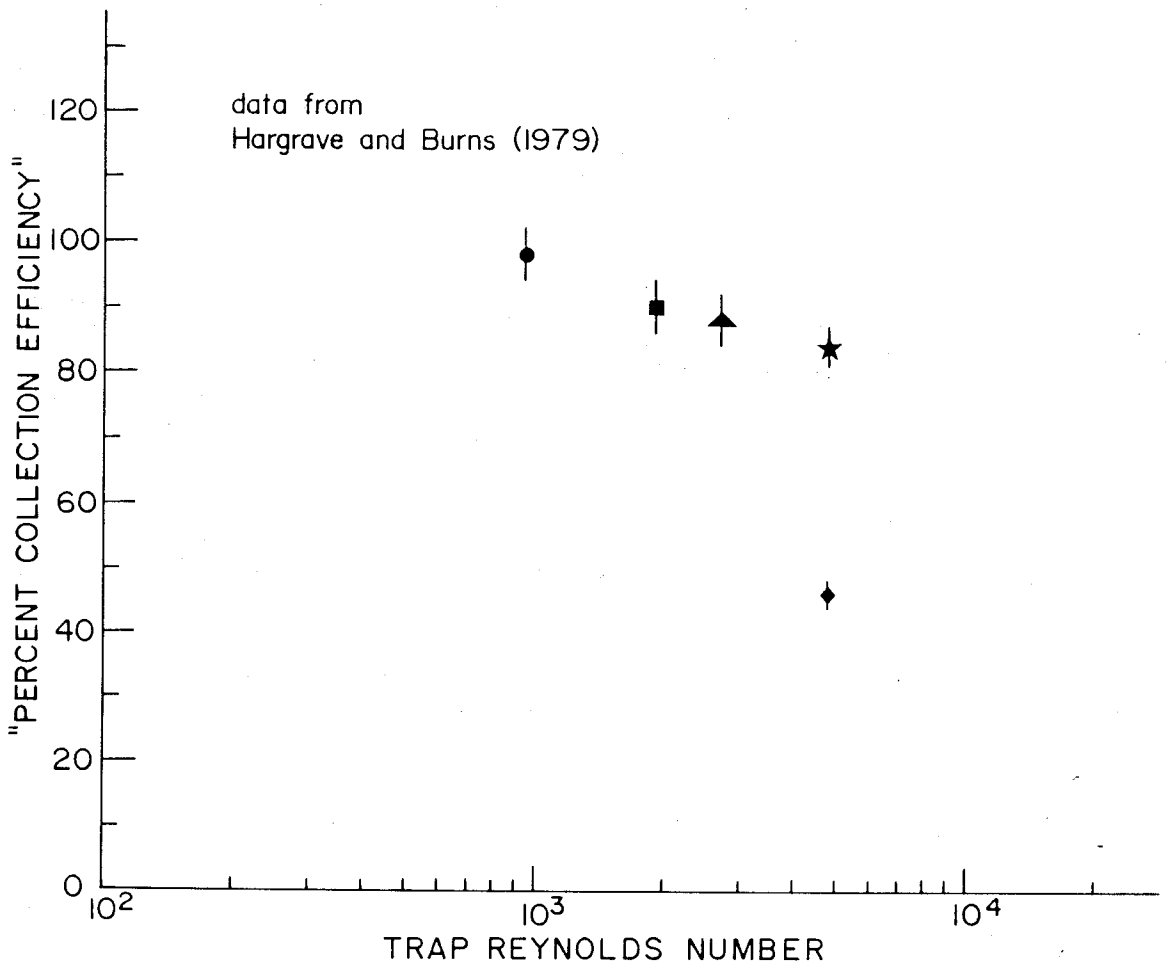


Figure 2.5: Effect of trap Reynolds number on "percent collection efficiency" in the seawater study of sediment collectors conducted by Hargrave and Burns (1979). Dimensions of the trap designs are given below Figure 2.8; data for their trap design 1 (circle), 2 (square), 3 (triangle), 4 (diamond) and 5 (star) are plotted here. Vertical bars represent 4 percent error around each point, the measurement precision for these trap tests as determined by Hargrave and Burns (1979). Traps were tested at flow speeds of 4 to 5 cm/sec ($V = 4.5$ cm/sec was used in R_t calculations). R_t were calculated as described in caption to Figure 2.1. The flow was seeded with natural sediments < 125 μm in diameter. "Percent collection efficiencies" were calculated as the weight of material deposited per unit area in the trap as a percentage of the "sedimentation rate" in the flume. The sedimentation rate was determined from "changes in the concentration of suspended matter in the tank."

bars overlapped for adjacent traps on the R_t scale; only cylinders with the smallest and the largest R_t have significantly different (i.e., nonoverlapping error bars) collection efficiencies. The cylinder with an aspect ratio of 1.2 collected significantly less material than the other traps, but this effect may be more strongly related aspect ratio than to R_t (see Section 2.3).

Results of Lau's (1979) study on water motion inside cylindrical traps clearly demonstrates an R_t effect; for a given aspect ratio, the degree of water motion at the trap bottom increases with increasing R_t. In the flume, Lau tested three cylinder diameters (3.4, 5.0, and 8.8 cm), having aspect ratios ranging from 4.7 to 10. He visually determined whether or not neutrally buoyant droplets, initially placed 1- to 2-cm above the trap bottom, stayed in the trap or escaped from the trap for R_t ranging from 2×10^3 to 3×10^4 (flow speeds of 3 to 75 cm/sec). The oil droplets eventually escaped from all the traps tested, but escape occurred at lower R_t for lower H/D (Figure 2.6). The aspect ratio effect is also described in Section 2.3.3.

2.3.2 Particle collection efficiency and the dimensionless velocity ratio

It is difficult to directly assess the effect of the dimensionless velocity ratio, u_f/W, on particle collection efficiency because W was not measured or estimated in any of the studies. However, a in particle sizes (usually particle diameters) used to seed the flows was given in each study. Particle fall velocity is a function of both particle density and particle

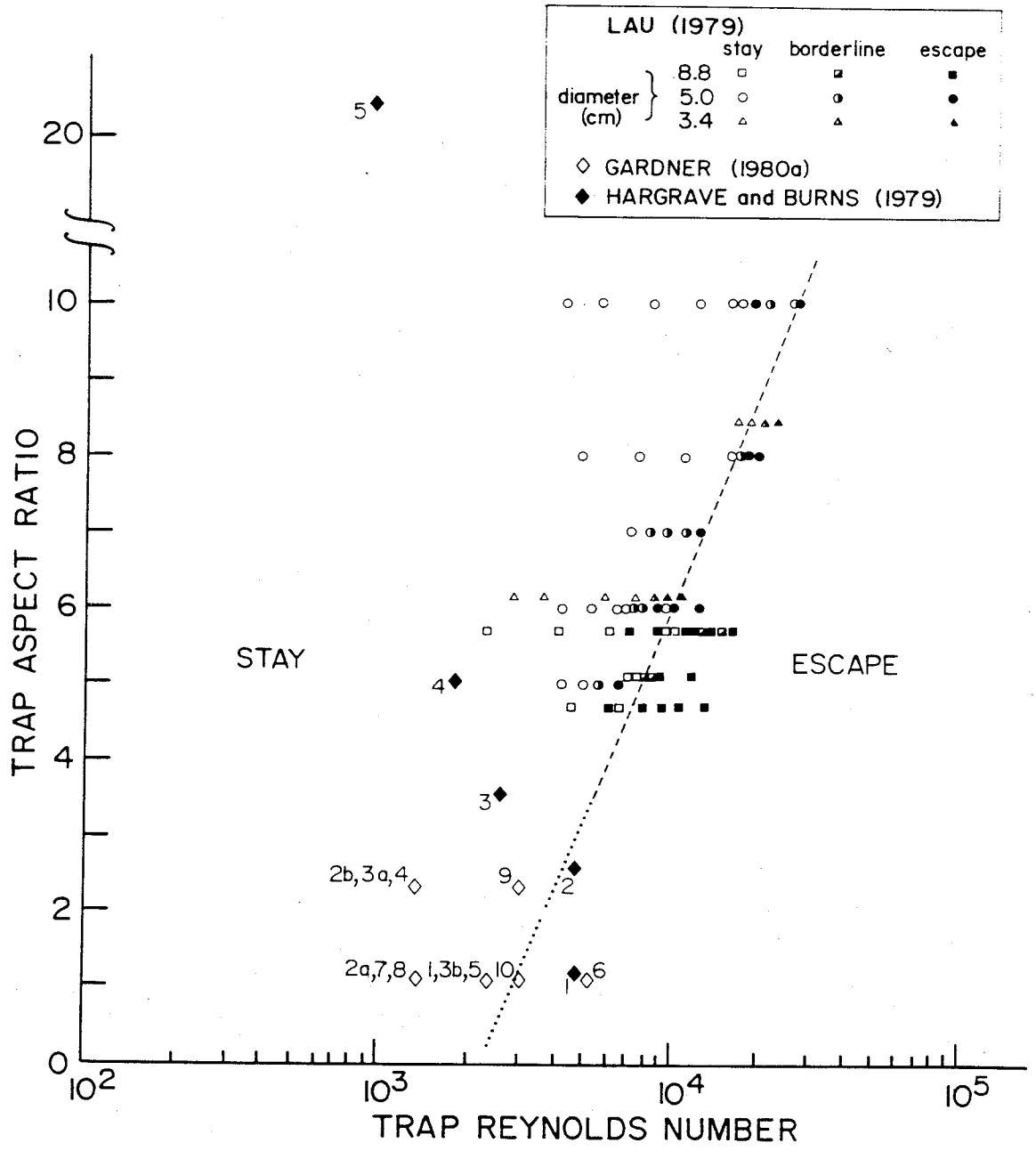


Figure 2.6: Behavior of oil droplets in the bottom of traps with various aspect ratios and R_t from the study of Lau (1979). "The dashed line indicates approximately the separation between the 'stay' and 'escape' regions" (Lau 1979). The dotted part is an extension, by the present author, of Lau's dashed line for lower aspect ratios and R_t. Also plotted on the Figure are data from Gardner's (1980a) and Hargrave's and Burns' (1979) studies of straight-sided cylinders. See Section 2.3.3 for description of the way that these data were plotted on Lau's graph.

diameter, but is more sensitive to changes in the latter because $W \propto d^2(\rho_p-\rho_f)$ for Stokes particles (see eq. 3.5). In addition, ρ_p of naturally occurring suspended particles in the ocean usually varies only between 1.0 and 3.0 g/cm^3 (e.g., quartz sand grains are considered relatively dense particles in the ocean and have $\rho_p \simeq 2.65$ g/cm^3) whereas d varies over several orders of magnitude (suspended individual particles can be any size from millimeters down to less than microns). Thus, in this section, the particle collection efficiency data from the published studies are discussed relative to the particle diameters used to seed the flows. Rough estimates of u_f/W are then calculated for the studies in an attempt to link any observed collection efficiency versus particle diameter effects with a particular range in u_f/W.

The importance of particle characteristics in determining particle collection efficiencies of traps is virtually unexplored quantitatively; however, the experimental information available indicates that trap efficiencies decrease with decreasing particle diameter, particularly at relatively low R_t. Tauber (1974) used three species of pollen spores in his calibration study; each species had a significantly different (i.e., nonoverlapping ranges) diameter from others (see Figure 2.2). At the lowest two R_t tested, the rank order of efficiencies mirrored the rank order of particle diameters (that is, efficiency decreased with decreasing R_t). However, at an R_t of ~ 3×10^4, the lines crossover and the efficiency slightly increased with decreasing particle diameter. Even though the rank order of efficiencies for the three spore diameters

remained constant for all four trap tests at $R_t > 3x10^4$, it is unclear whether or not the efficiencies are actually significantly different from each other (Tauber did not indicate the measurement error for these experiments).

During calibration experiments, Peck (1972) also used several pollen diameters, but pollen from different genera were used in each run. For the two R_t tested, the rank order of collection efficiencies coincided with the rank order of grain diameters (see Figure 2.3); the larger grain diameters at a given R_t were collected more efficiently than were the smaller grain diameters. Also, the magnitude of efficiency differences between grain diameters decreased with increasing R_t.

Neither Tauber (1974), nor Peck (1972) determined the fall velocities of the pollen they tested. Peck listed, from the literature, the average "densities" (these may actually be specific gravities because no units for the "densities" are given in Table 3, page 194 of Peck [1972]) of five of the spores tested. These values do not increase with increasing spore diameter. However, the "densities" listed for two of the genera (Dactylis and Pinus) were less than one. These spores should not have sunk in water. Peck stated that, in the experiments, pollen was added to the weir end of the flume where "it became wetted." In fact, many pollen grains have air spaces inside and do not sink until water can enter these spaces or they are "wetted" (e.g., see Hopkins 1950 and Reynolds 1979). For example, Reynolds (1979) boiled previously dried pollen of Lycopodium to thoroughly wet it before additions to freshwater. Thus, the

"densities" provided by Peck are probably meaningless for determining the physical characteristics (such as Stokes' fall velocities) of wetted pollen sinking in water. Fall velocities of pollen in water must be determined directly on the wetted grains.

Fall velocities of pollen in air (applicable to Tauber's 1974 study) can be calculated from the "density" values provided by Peck (1972). The studies of Peck and Tauber had only one pollen genus in common, Lycopodium. Using the "density" of 1.175 [g/cm^3] given by Peck for Lycopodium (Peck cited Zeleny and McKeehan 1910, for this value, but see also the density values calculated by Reynolds 1979), then $W = 2.46 \times 10^{-2}$ cm/sec, as calculated from Stokes equation (see eq. 3.5 in Section 3.2.7) for $d = 26.3$ μm, $\mu_f = 1.8 \times 10^{-4}$ g/cm sec, and $\rho_p = 1.20 \times 10^{-3}$ g/cm^3. Thus, the ratio of u_f/W is 4.1×10^3 to 4.1×10^4 for Tauber's wind-tunnel tests of Lycopodium (at wind speeds of 100 to 1000 cm/sec).

The ratio of u_f/w also can be determined for flume tests of Lycopodium in Peck's (1972) study because Reynolds (1979) directly measured the sinking rate of wetted Lycopodium spores. For Reynolds' measured W of 1.33×10^{-3} cm/sec (see Reynolds' Table 1, page 60), u_f/W is 9.7×10^3 to 1.9×10^4 for this pollen genus falling through water in Peck's study.

The relationship between particle characteristics and particle collection efficiencies cannot be assessed for the two sediment trap studies (Gardner 1980a, Hargrave and Burns 1979). Both studies used mixtures of natural sediments to seed the flow; particle sizes in these mixtures spanned wide ranges (particles < 63 μm were used in

Gardner's study and particles < 125 μm were used in Hargrave's and Burns' study). Because the particle size distributions in the oncoming flow or in trap samples were not determined in either study, the possibility of particle size selection by certain trap designs or in certain R_t flows cannot be assessed. A lower limit for u_f/W was determined for the two sediment trap studies (see Table 2.1) by using the calculated W (from Stokes' equation, see eq. 3.5) for roughly the largest particle size (and assuming $\rho_p \simeq 2.65$ g/cm^3, and values for ρ_f and μ_f for freshwater at 20°C and one atmosphere) and the lowest flow speed tested in each study (4.0 cm/sec).

In Gardner's study, 95 percent of the particles used to seed the flow were < 25 μm (as determined by Coulter Counter analysis) so $u_f/W = 77$ for d = 24 μm and W = 0.052 cm/sec. In Hargrave's and Burns' study, particles < 125 μm were used to seed the flow (no other information is given about the sediment mixture) so $u_f/W = 2.9$ for d = 124 μm and W = 1.38 cm/sec.

2.3.3 Particle collection efficiency and trap aspect ratio

Evidence that collection efficiencies of cylinders are a function of both trap aspect ratio (H/D) and R_t comes from the study of Lau (1979). Lau's experimental design and results, primarily in relation to R_t, were described in Section 2.3.1. The combined R_t and aspect ratios effects are discussed here. The data indicated that, for higher R_t, traps with higher aspect ratios were required to prevent the escape of oil droplets from the trap (Figure 2.6). For example, at $R_t \simeq 6 \times 10^3$ oil droplets escaped from a trap 5 cm in diameter with an aspect ratio of 5, but the droplets

stayed in traps with aspect ratios of 6, 7, 8 and 10. For these traps, oil droplets escaped at $R_t \geq 9x10^3$, $\geq 1x10^4 \geq 2x10^4$, and $\geq 3x10^4$, respectively. At $R_t \leq 6x10^3$, the oil droplets essentially remained in all traps with aspect ratios ≥ 4.7 (traps with aspect ratios < 4.7 were not tested). At $R_t \simeq 1.8x10^4$, the oil droplets stayed only in traps with aspect ratios of 8.4 to 10, but escaped from traps with aspect ratios of 4.7 to 8.4. Lau's study did not provide information on particle movement under these conditions.

Both sediment trap studies (Gardner 1980a; Hargrave and Burns 1979) investigated the effect of aspect ratio on particle collection efficiencies of cylinders. However, results of these studies are difficult to compare with Lau's (1979) results because, (1) Gardner did not test aspect ratios > 2.3 and the range in R_t for the traps tested was $1.3x10^3$ to $5x10^3$ (see Figure 2.6) and (2) for all aspect ratios (ranging from 1.2 to 20.4) tested by Hargrave and Burns, trap diameter decreased with increasing aspect ratio (except for traps with aspect ratios of 1.2 and 2.8) so that the two traps with aspects ≥ 4.7 had R_t of $9.5x10^3$ and $1.9x10^3$ (see Figure 2.6).

In Gardner's (1980a) study, no effect of aspect ratio on collection efficiency is apparent for aspect ratios ranging from 1 to 2.3 at any of the R_t tested (Figure 2.7). However, for each aspect ratio, an increase in R_t by about a factor of two also increased particle collection efficiencies by 20 to 40 percent (compare experiment 5 with the other experiments in Figure 2.7). These results may not be significant because the between-replicate

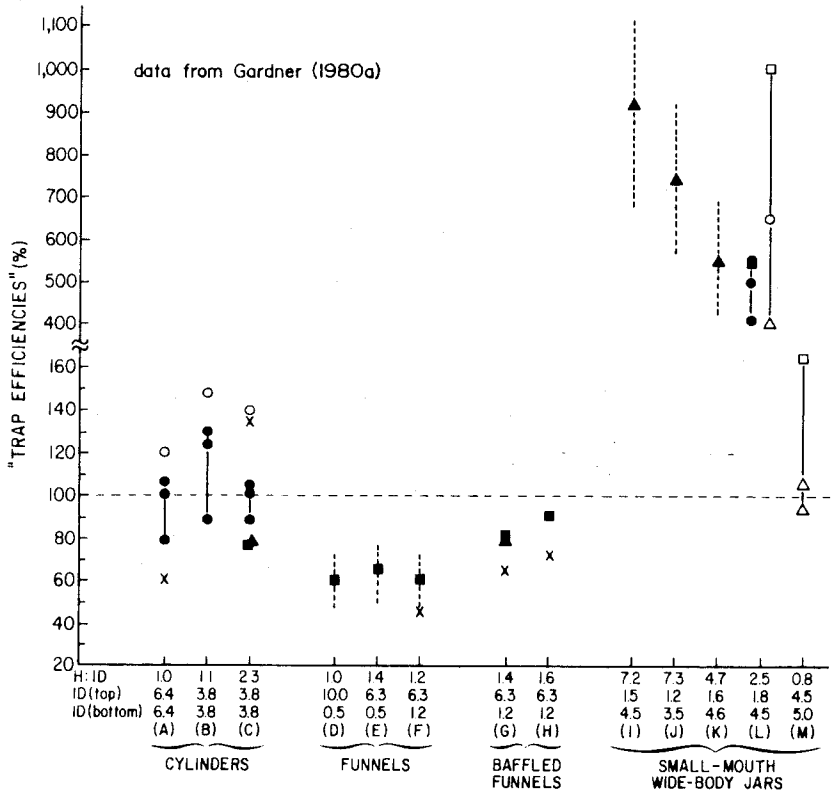


Figure 2.7: "Trap efficiencies" of several trap designs tested in the laboratory flume study of Gardner (1980a). "Trap efficiencies" (defined in Figure 2.4) were taken from his Tables 3, 4, and 5 (pages 24-26) and are based on A_m (trap mouth area). Relevant trap dimensions (in cm) were taken from his Table 1 (page 21) and appear below this figure; the baffle cells were 1-cm high and 1-cm wide. The trap designs are labeled here by the letters A through M (appearing in parentheses below the Figure). The points plotted in this figure were taken from nine separate flume experiments. The flow was seeded with natural sediments < 63 μm in diameter (95 percent were < 26 μm in diameter). The flow speeds (in cm/sec) and particle concentrations (in mg/l) for these experiments (taken from Gardner's Tables 3, 4, and 5) were, respectively: 9.0 and 11.8 for experiment 1 (open triangles), 8.9 and 11.5 for experiment 2 (open squares), 4.4 and 51.0 for experiment 3 (closed circles), 4.4 and 55.0 for experiment 4 (closed circles), 9.5 cm/sec and 58.2 for experiment 5 (open circles), 4.4 and 53.0 for experiment 6 (closed circles), 4.3 and 34.4 (also, traps were rotated during this experiment) for experiment 8 (crosses), 4.0 and 31.2 for experiment 9 (closed squares) and 4.0 and 82.4 for experiment 10 (closed triangles). Experiments 3, 4 and 6 are not distinguished in this figure (i.e., they are all indicated by closed circles) because the conditions were approximately replicated between these experiments. Trap efficiencies determined under similar experimental conditions (as judged by the author) are connected by solid vertical lines in this figure. Dotted lines represent an estimated CV of 23 percent surrounding the data point (as calculated in Section 3.4.4).

variability in trap collections was potentially high (ranging from 9.4 to 44.6 percent, see Section 3.4.4) in Gardner's study.

In Hargrave's and Burns' (1979) study, at the same R_t (of 4.8×10^3) traps with aspect ratios of 1.2 and 2.8 differed in efficiency by about a factor of two, the lower efficiency associated with the lower aspect ratio (Figure 2.8). With increasing aspect ratios from 2.6 to 20.4, efficiencies slightly increased, but only the efficiency for the trap with an aspect ratio of 20.4 can be considered significantly higher than the others (based on the criteria of nonoverlapping error bars). Baffling a cylinder with an aspect ratio of 4.0, with several sizes of baffles, increased the cylinder's collection efficiency by about 20 percent. As previously noted, the increasing aspect ratios also had decreasing R_t so the results are difficult to interpret.

The aspect ratio data of Gardner (1980a) and of Hargrave and Burns (1979) are qualitatively compared to Lau's (1979) results in Figure 2.6. Here, all of the cylinders tested in each of the two sediment trap studies were ranked (separately for each study) in order of increasing collection efficiency. Each rank is plotted on the figure by its coordinates for R_t and aspect ratio. Of all the cylinders tested in the two sediment trap studies, only four fall to the right of an extension of Lau's dashed line dividing the approximate "separation between the 'stay' and 'escape' regions" for oil droplets in his traps.

If water velocities at the trap bottom, that entrain the oil droplets and allow them to escape from a trap, can also generate

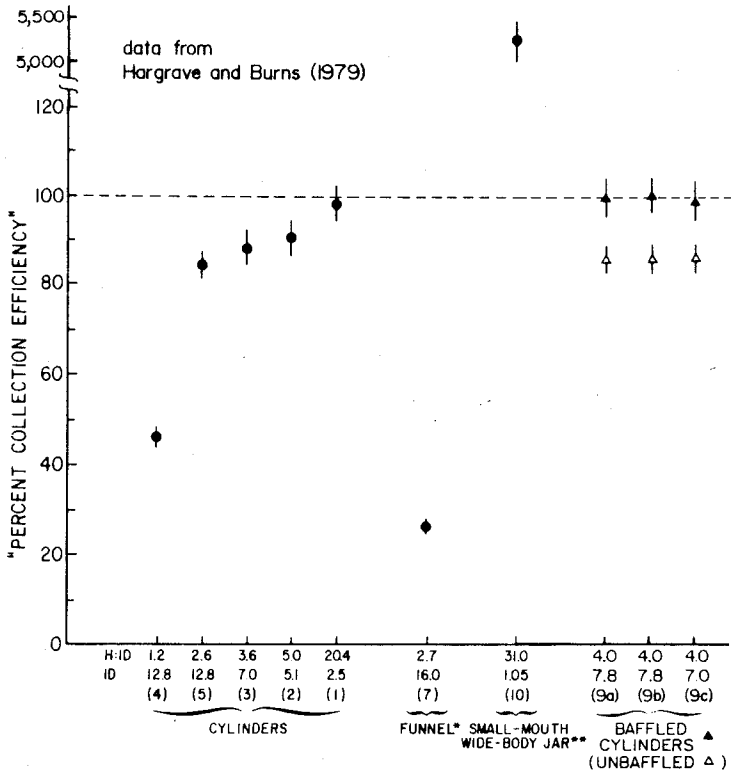


Figure 2.8: "Percent collection efficiency" of several trap designs tested in the laboratory flume study of Hargrave and Burns (1979). Except for trap 10, "Precent collection efficiencies" (defined in Figure 2.8) were taken from their Figure 2 (page 1130) and are based on A_m (trap mouth area). The "precent collection efficiency" for trap 10 was calculated from the value plotted on their Figure 2 (page 1130), using A_m in the calculation (they used A_b in their efficiency calculation for this trap design). Relevant trap dimensions (in cm) were taken from their Figure 1 (page 1128) and appear below this figure. All traps were tested simultaneously at a flow speed of 4 to 5 cm/sec; the flume was seeded with natural sediments < 125 μm in diameter. Vertical bars are 4 percent error bars around each point, the measurement precision for these trap tests as determined by Hargrave and Burns (1979). The diameters and H:ID ratios of the baffles inserted into trap 9 were 0.64 cm and 48 for trap 9a, 0.87 cm and 36 for trap 9b and 1.91 cm and 16 for trap 9c. *This funnel-trap consisted of a funnel (16.0-cm inside mouth diameter, < 1.0-cm inside diameter at bottom, and 18.0-cm tall) inserted into a cylinder (7.0-cm inside diameter and 25.5-cm tall); the cylinder mouth was sealed to a < 1.0-cm opening surrounding the bottom of the funnel. **This trap was a cylinder (7.8-cm inside diameter and 32.5-cm tall) covered by a watch glass cover (8-cm diameter) with a central hole (1.05-cm diameter). () = trap number designated by Hargrave and Burns in their Figure 1 (page 1128).

sufficient turbulence to resuspend settled sediments, then traps falling to the right of Lau's dashed line (Figure 2.6) should be relative undercollectors compared with traps falling to the left of the line. Lau's line, and the present author's extension of Lau's line divide the cylinders tested by Hargrave and Burns between the aspect ratios of 2.6 and 3.6; however, in plots of these data where R_t is ignored (Figure 2.8), the collection efficiencies for these two aspect ratios cannot be considered significantly different. Most of Gardner's data fall to the left of the present author's extension of Lau's line and the two data points falling to the right of this line had relatively high particle collection efficiencies; this suggests that the resuspension has a negligible effect on particle collection efficiency for these low aspect ratios (between 1.0 and 2.3) at low R_t.

Clearly, ambiguities exist in the data between the studies of Gardner (1980a), Hargrave and Burns (1979) and Lau (1979); it is emphasized here that the data should not be interpreted too literally because of the many differences between the studies (e.g., in experimental design, methodologies, and particles used to see the flows). In addition, Lau's dashed line was fit to the data by eye, not by any statistical technique. Several lines of various slopes would, in fact, fit the data equally as well as the one shown in Figure 2.6. Also classifying Gardner's and Hargrave's and Burns' data in this manner assumes that the present author's simple extrapolation of Lau's straight line on a semi-log plot (Figure 2.6) is reasonable and physically justified.

Peck (1972) looked at the effect of aspect ratio on particle

collection efficiency of the Tauber trap (diagramed in Figure 2.2) by testing a "short" (6-cm tall, aspect ratio = 1.2, using the mouth diameter of 5 cm) and a "tall" (10-cm tall, aspect ratio = 2.0) version of this trap design for R_t of 2.2×10^4 to 4.2×10^4. The tall trap always collected more pollen per unit area than the short trap, but the mean difference between the two trap designs was only about 15 percent.

All of the data do suggest that resuspension of particles in the bottom of straight-sided cylinders and in the Tauber trap, with relatively low aspect ratios, may occur, thereby decreasing particle collection efficiencies. The aspect ratios required to prevent significant resuspension are evidently R_t-dependent. However, the exact quantitative relationships between R_t, aspect ratio, and particle collection efficiency require elucidation through experimentation.

The studies of Hargrave and Burns (1979) and Peck (1972) indicate that collection efficiencies are relatively low for aspect ratios of ~ 1.0 compared to aspect ratios of ~ 2.0, but Gardner's (1980a) data do not support this trend. Only slightly higher efficiencies were achieved for aspect ratios from 2.6 to 20.4 in Hargrave's and Burns' study, but interpretation of these results is difficult because the higher aspect ratios also had lower R_t. Lau's (1979) study showed that, for increasing R_t, water motion in the bottom of traps occurs at higher aspect ratios, indicating that traps with relatively high aspect ratios may be required to prevent resuspension of particles from the trap bottom at relatively high R_t.

Water motion by itself does not indicate that resuspension will occur. Some measure of a ratio of critical entrainment stress to resisting force, such as Shields' parameter (Shields 1936), is necessary to quantify the values of stress, sediment density and size which are stable or unstable in a given flow. Velocities, turbulent intensities or values of shear stress are not available from Lau's experiments.

The R_t tested in Lau's study were higher than the R_t tested in the two sediment trap studies ($2x10^3$ to $3x10^4$ for Lau's study versus $9.5x10^2$ to $5x10^3$ for the two sediment trap studies). Peck's study was conducted over a range of R_t ($2.2x10^4$ to $4.2x10^4$) similar to Lau, but Peck did not test straight-sided cylinders. In addition, Lau tested higher aspect ratios than were tested in the other studies; only two traps out of all the traps tested by Gardner, Hargrave and Burns, and Peck had aspect ratios within the range of those tested by Lau. Without experimental confirmation, it is not valid to simply extrapolate Lau's results for values of H/D and R_t that are outside the range that was actually tested. In addition, as discussed above, Lau's study provides no information on particle resuspension in traps. Thus, the only reasonable conclusion from these data sets is that the effect of aspect ratio on particle collection efficiencies of traps must be empirically determined for a realistic range of R_t.

2.3.4 Particle collection efficiency and trap geometry

The two sediment trap studies (Gardner 1980a; Hargrave and Burns 1979) investigated the effect of trap geometry on particle collection

efficiency, while Peck (1972) and Tauber (1974) measured collection efficiencies only for the Tauber trap and Lau (1979) looked only at cylinders. The results for two kinds of trap designs (funnels and small-mouth wide body traps), other than cylinders, tested by Gardner (1980a) and by Hargrave and Burns (1979) are described here.

In Gardner's study, funnels had lower collection efficiencies, by about 30 percent, than cylinders with similar aspect ratios and/or mouth diameters (compare especially funnel traps E and F with cylinder A in Figure 2.7). Baffling the mouth opening of these funnels raised their collection efficiencies to within the range of the cylinder collection efficiencies. All small-mouth wide-body traps, except one, had higher collection efficiencies by factors of four to ten compared to the cylinders (Figure 2.7). However, the mouth diameters, and thus the R_t, of these small-mouth wide-body traps were at least half the mouth diameters of the cylinders. The one small-mouth wide-body trap (trap M in Figure 2.7), which had a collection efficiency similar to the cylinders, also had a mouth diameter similar to the cylinders and had the highest ratio of inside diameter at the mouth to inside diameter at the bottom of the trap (0.90 compared to 0.33-0.40 for traps I, J, K and L in Figure 2.7).

The funnel trap tested by Hargrave and Burns (1979) collected 50 to 80 percent less material per unit area than the cylinders tested (Figure 2.8), but the funnel trap also had the largest R_t of all traps tested. The one small-mouth wide-body trap tested by Hargrave and Burns had a remarkably high collection efficiency. This small-mouth wide-body trap had the lowest R_t and the highest aspect

ratio of all traps tested by Hargrave and Burns.

The behavior of the funnels with and without baffles suggests that resuspension of particles settling on the funnel wall may occur. The baffles tend to dampen the large energetic eddies and, therefore, reduce the potential for resuspension and transport of particles out of the trap. This idea remains to be conclusively demonstrated by direct experimentation.

For all of the trap designs discussed here, where $A_m \neq A_b$, (A_m = area of trap mouth and A_b = area of trap bottom), if A_b (or, for some of the funnel traps, the area at the bottom or neck of the funnel) is used instead of A_m in collection efficiency calculations, most small-mouth wide-body traps have collection efficiencies between 60 and 100 percent, while the funnel traps have unusually high collection efficiencies, of 1,600 to 24,000 percent (Table 2.3). The implications of these results are discussed later (Section 2.4.5).

2.3.5 Limitations to these studies

Particle collection efficiencies determined in the four studies (Peck 1972, Tauber 1974, Gardner 1980a and Hargrave and Burns 1979) discussed in Sections 2.3.1 through 2.3.4 cannot be compared between studies. In addition, the measured collection efficiencies in these laboratory studies should not be directly extrapolated to the field. The studies are not comparable because, for each experiment, collection efficiencies could be calculated only as a function of a limited range of parameters (see Section 2.2 and Table 2.1) which were different in each study (see also captions to Figures 2.2, 2.3,

TABLE 2.3

Particle Collection Efficiencies of Noncylindrical Traps Using an Inside Diameter, other than at the Trap Mouth, in Calculations, for the Studies of Gardner (1980a) and Hargrave and Burns (1979)

Trap[1] design	Inside diameter at mouth (cm)	Collection[2] efficiency (percent)	Inside diameter[3] below mouth (cm)	Collection[4] efficiency (percent)
Small-mouth wide-body traps				
I	1.5	896	4.5	100
J	1.2	743	3.5	87
K	1.6	554	4.6	67
L	1.8	413	4.5	66
		550		88
		651		104
		508		81
		391		63
		994		159
M	4.5	106	5.0	86
		94		76
		163		132
10	1.05	5198	7.8	94
Funnel traps				
D	10.0	60	0.5	24000
E	6.3	65	0.5	10319
F	6.3	65	1.2	1654
7	18.0	26	< 1.0	5156

1. The trap designs corresponding to the letters listed here are given in Figure 2.7 (for the study of Gardner 1980a) and the trap designs corresponding to the numbers listed here are given in Figure 2.8 (for the study of Hargrave and Burns 1979).
2. These are the "Trapping Efficiencies" given by Gardner (1980a) for all lettered traps listed here and the "Percent Collection Efficiencies" given by Hargrave and Burns (1979) for trap 7; the efficiencies were calculated for A_m. For trap 10, the value listed here was calculated from the efficiency given by Hargrave and Burns (listed in the fifth column of this table).
3. These are the body diameters for the small-mouth wide-body traps and the diameters at the bottom or neck of the funnels.
4. These were calculated for all traps, except one (trap 10), from the values listed in the third column of this table. For trap 10 this is the "Percent Collection Efficiency" given by Hargrave and Burns (1979), based on A_b.

2.4 and 2.5). Results of the studies cannot be applied directly to the field because laboratory and field environments differ in, (1) particle characteristics (especially in the range of particle fall velocities and in particle concentrations), and (2) flow characteristics (e.g., the unsteadiness of the flow and the level of turbulence).

Results of the studies also must be interpreted conservatively because of limitations to various aspects of the experimental design and of the procedures used in the studies. In Section 3.1.2, criteria are outlined for designing and conducting laboratory experiments on traps to, (1) satisfy geometric and dynamic similarity between field and laboratory tests, and (2) minimize experimental error. The problem of laboratory R_t being smaller than field R_t for the sediment trap studies was discussed in Section 2.3.1 (but see also Criteria A in Section 3.1.2). Examples of some other specific limitations to Gardner's (1980a) study are discussed below. In most cases, it is not possible to make a posteriori evaluations of the exact effects on particle collection efficiencies. Rather, the foregoing discussion suggests that error bars may be large around some of the measured efficiencies; certain inconsistencies in the data both within and between studies should not be interpreted too literally. The major point of this discussion is to emphasize that the five pioneering calibration studies (Peck 1972; Tauber 1974; Gardner 1980a; Hargrave and Burns 1979; Lau 1979), summarized here, have made valuable contributions toward our understanding of sediment trap biases, but the studies have, for the most part, raised more

questions than they have answered. The groundwork laid down by these studies is an invaluable resource for making a priori hypotheses (some of which are presented in Section 2.4) to test in future laboratory studies of particle collecting traps.

Certain aspects to the flume design and placement of traps in the flume in Gardner's (1980a) study indicate that the error bars on his efficiency estimates may be large. The boundary layers on the bottom and side walls of his flume may have interacted with the trap causing disturbances to the supposedly "steady, uniform flow"; perculiar patterns of secondary circulation in the vicinity of the traps may have occurred. In addition, the evidence (given below) suggests that each trap was collecting particulates in a different flow regime and that the traps were experiencing different shear forces in the flow. (These effects are described in more detail in Criteria B, Section 3.1.2).

Gardner's (1980a) flume was 17-cm wide and the diameters of traps, with circular mouth openings, tested in the flume ranged from 1.2 to 10 cm (these are inside diameters, Gardner did not list outside diameters in his Table 1, page 21). Half of the traps tested in his flume were less than three trap radii from each flume side wall; in fact, $\leq$ 1.7 trap radii were between the side walls and six out of 14 of the traps. From potential (frictionless) flow theory it can be shown that at a cross-stream distance of three radii from a cylinder there is only about an 11 percent increase in the free-stream velocity, but at a distance of 1.7 trap radii from the cylinder, the velocity is ~ 35 percent higher than the free-stream

value. Thus the flow was significantly accelerated around many of the traps tested by Gardner; in addition, the flow was nonuniform in the cross-stream direction.

Gardner's flume was six meters long and up to eight traps, in a linear array, were tested in the flume at a time, each trap separated from adjacent traps by 60-70 cm. The calculated boundary layer thicknesses various distances along the flume bed and side walls (i.e., distances from the flow source) are listed in Table 2.4 for laminar and for turbulent flows over a flat plate. These thicknesses range from 10 to 100 percent of the flume depth (15 cm) and from 18 to 100 percent of the flume width. Thus, each trap in a linear array collected particulates in a different portion of the bottom or side-wall boundary layers; thus, each trap experienced different shear forces in the flow. In addition, the curved streamlines of flow moving around the traps (see Criteria B, Section 3.1.2) may have interacted with the side-wall boundary layers producing peculiar circulation effects. Gardner tested the effect of changing the order of the traps in one of the linear arrays and found that collection efficiencies changed by 8 to 30 percent (Gardner 1977). In addition to boundary-layer effects, these results suggest that the disturbed flow downstream of each trap may not have recovered to its predisturbed state before encountering the next trap in the array. In summary, some relative increases or decreases in particle collection efficiencies between trap designs may have resulted, at least in part, from their relative positions in the flume during experiments.

TABLE 2.4

Calculated Boundary-Layer Thickness (δ) in the FLume and for the Flow Speeds used by Gardner (1980a)

Distance (x) from flow source (cm)	Re_x[1] for u = 4.0 cm/sec	δ for laminar flow[2] (cm)	δ for turbulent flow[3] (cm)	Re_x[1] for u = 9.5 cm/sec	δ for laminar flow[2] (cm)	δ for turbulent flow[2] (cm)
50	1.1×10^4	2.4	2.1	2.6×10^4	1.6	1.9
100	2.2×10^4	3.4	3.8	5.1×10^4	2.2	3.4
200	4.3×10^4	4.8	7.0	1.0×10^5	3.1	6.2
300	6.5×10^4	5.9	9.8	1.5×10^5	3.8	8.7
400	8.6×10^4	6.8	12.6	2.0×10^5	4.4	11.1
500	1.1×10^5	7.6	15.3	2.6×10^5	4.9	13.5

1. $Re_X = (x)(u)/\nu$, where x = distance from flow source, u = mean stream velocity of the flow, and $\nu = 1.185 \times 10^{-2}$ cm^2/sec (30 ppt seawater at 20°C and one atmosphere).
2. $\delta \simeq (x)(5.0)(Re_X)^{-1/2}$ according to the Blasius profile (e.g., see White 1979, page 400) for flow across a flat plate.
3. $\delta \simeq (x)(0.16)(Re_X)^{-1/7}$ (e.g., see White 1979, page 400) for flow across a flat plate.

2.4 Hypothesized Biased Trapping Effects, Based on Theoretical Considerations and on Results of the Published Laboratory Studies of Trapping Characteristics

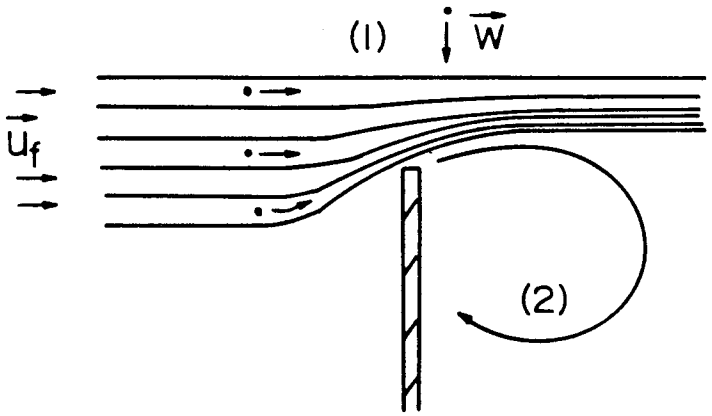
Developing a set of working a priori hypotheses before investigating any scientific phenomenon serves to, (1) summarize the available data base, (2) organize the research such that each experiment tests a specific hypothesis and, thus, a specific mechanism, (3) streamline the number of experiments that must be conducted and (4) help insure that the proper variables will be measured in the experiments so that a definitive statement can be made regarding the feasibility of any hypotensis tested. To understand the complex process of trapping particulates in marine environments, the system initially must be simplified so that specific mechanisms can be tested. Thus, the first three hypotheses presented here (in Sections 2.4.2, 2.4.3 and 2.4.4) are for straight-sided cylindrical traps. The other hypotheses (presented in Section 2.4.5) concern the effects of noncylindrical trap geometries on particle trapping. For all theoretical models presented here, the flow field is limited to two dimensions; the cross-stream component of the flow is ignored. Also, fluid buoyancy effects are ignored (e.g., Gardner's [1977] theoretical description of overcollection by small-mouth wide-body traps summarized in Section 2.1.2) because particle concentrations that effect fluid buoyancy are too large (of the order 10^{-3} volume concentration [Smith and McLean 1977; Grant and Glenn 1983]) to be relevant to trap collections in most oceanic systems.

The hypotheses were stipulated both from the dimensional analysis (presented in Section 2.2), indicating parameters likely to effect particle trapping, and on results of the published laboratory studies of trapping characteristics (presented in Section 2.3). The hypotheses are not necessarily supported by all of the data in the laboratory studies; however, each hypothesis is solidly supported by data from at least one of the studies. No attempt is made here to explain deviations, in the published studies, from the proposed hypotheses. As previously discussed (Section 2.3.5), certain ambiguities in data both within and between studies may be expected because of problems in experimental design and because all of the studies tested different particle types, trap designs, and R_t. To properly test the hypotheses presented here, relatively rigorous laboratory experimentation is required.

As background for the theoretical models and mechanisms presented in Sections 2.4.2 through 2.4.5, first (in Section 2.4.1) the general process of trapping particulates is described, based on observations of flow through traps (e.g., dye studies) and on the mass balance for particles entering and leaving traps. Any proposed mechanism to explain a trap bias must affect one or more terms in the mass balance. The terms affected by each mechanism and the resultant relative changes in collection efficiency are described in Sections 2.4.2 through 2.4.5.

2.4.1 Background theory

During particle trapping, trap-induced flow accelerations occur in two ways (refer to Figure 2.9). First, the oncoming flow locally



(1) Local acceleration of flow around trap; compression of streamlines of flow

(2) Boundary layer forms over trap mouth; pressure drag causes flow to separate shedding an eddy into trap

Figure 2.9: Diagram of two-dimensional flow past the vertical wall at the mouth of a cylinder, showing flow accelerations.

accelerates as it changes direction to move over or around the trap. Second, turbulent eddies can be shed over the trap mouth. An internal boundary layer forms over the trap due to the drag of the trap on the flow. If the adverse pressure gradient is large enough, separation of the flow occurs at the leading edge of the trap mouth and the flow near the boundary reverses direction. In this way, eddies are shed over the trap mouth. Dye studies have demonstrated eddy shedding over straight-sided cylinders for R_t of about 3.8×10^2 to 9.6×10^3 (Gardner 1977, 1980a) and of about 1.3×10^3 to 1.1×10^4 (present study, see Section 3.3.7 and the photographs presented in Figures 3.35 through 3.41) and over Tauber traps for R_t of 2.2×10^4 to 4.3×10^4 (Peck 1972).

Particles are carried by the fluid only if the response time of the particles to changes in flow speed is very small, i.e., as long as particles follow the flow. It can be shown (see Appendix I) that the particles of interest in this study do accelerate nearly instantaneously with an accelerating flow field. However, one exception may be the behavior of particles in eddies shed into the trap mouth, where particle inertia, although small, may still be sufficient such that particle paths deviate slightly from fluid paths. Particle behavior in eddies is described in more detail in Section 2.4.2.

As Bloesch and Burns (1980) indicated in their analysis, traps potentially collect particles by two different mechanisms, (1) particles fall directly into the trap mouth and are retained on the bottom of the trap and (2) particles are carried into the trap by the

flow and then settle onto the trap bottom. Particles leave the trap only by being carried out with the flow. Assuming steady state, the total mass balance is described by the following equation

$$C_o W A_m + C_o Q + \phi_b A_b = C_t W A_b + C_t Q \qquad (2.3)$$

total mass added to trap interior per unit time = total mass leaving trap interior per unit time

where C_o = concentration of particles in the flow outside a trap (assuming a uniform particle distribution), C_t = concentration of particles inside a trap, ϕ_b = mass flux of particles resuspended from the trap bottom, Q = volume flux of fluid through the trap, A_b = area of trap bottom, A_m = area of trap mouth, and W = particle fall velocity. The three terms on the left-hand side of eq. 2.3 describe the total mass added to the trap interior per unit time: $C_o W A_m$ = flux of particles falling into the trap mouth, $C_o Q$ = flux of particles carried into the trap by the flow (i.e., particles entering with an eddy), and $\phi_b A_b$ = flux of particles resuspended from the trap bottom. The two terms on the right-hand side of eq. 2.3 describe the total mass leaving the trap interior per unit time: $C_t W A_b$ = flux of particles settling onto (i.e., "collected") on the trap bottom, and $C_t Q$ = flux of particles leaving the trap with the flow (i.e., carried out when the eddy leaves the trap). Equation 2.3 differs from the mass balance given by Bloesch and Burns (1980) only in the description of the resuspension term.

The particle collection efficiency (E) of a trap is defined as the net deposition of particles on the trap bottom divided by the

settling rate of particles through the trap mouth area,

$$E = \frac{C_t W A_b - \phi_b A_b}{C_o W A_m} \quad . \tag{2.4}$$

Assuming that the concentration of particles inside the trap (C_t) is fully mixed and uniform, eq. 2.3 can be solved for C_t; substitution of this solution into eq. 2.4 yields,

$$E = \frac{1 + (\frac{Q}{WA_m})\ (1 - \frac{\phi_b}{C_o W})}{1 + (\frac{A_m}{A_b})\ (\frac{Q}{WA_m})} \tag{2.5}$$

If $A_m = A_b$, then

$$E = \frac{(1 + \frac{Q}{WA_m}) - (\frac{\phi_b}{C_o W})\ (\frac{Q}{WA_m})}{(1 + \frac{Q}{WA_m})} \tag{2.6}$$

that is, E will be less than one due only to the loss of particles resuspended from the trap bottom and carried out by the flow. If resuspension is negligible (i.e., if $\phi_b = 0$) then $E = 1$ in eq. 2.6. The consequences to E just for the case where $A_b \neq A_m$ (i.e., assuming that resuspension is negligible) is evident from the following modification of eq. 2.5, where

$$E = \frac{1 + (\frac{Q}{WA_m})}{1 + (\frac{A_m}{A_b})\ (\frac{Q}{WA_m})} \tag{2.7}$$

Clearly, if $A_b < A_m$ then $E < 1$ and if $A_m < A_b$ then $E > 1$, for the definition of E given in eq. 2.4. This points out the importance

of how E is defined in determining whether a trap overcollects or undercollects particles.

2.4.2 Particle collection efficiency should decrease over some range of increasing trap Reynolds number

This hypothesis is qualitatively supported primarily by the results of Tauber (1974) and Peck (1972), for collections with the Tauber trap (see Section 2.3.1). In addition, the dimensional analysis (Section 2.2) suggested that collection efficiency would be a function of R_t. Several mechanisms can potentially cause a Reynolds-number dependence in particle trapping. Four mechanisms are examined here: the "Resuspension Mechanism," the "Trap Wall Surface Area Effect," the "Aggregation Model" and the "Eddy Model."

Resuspension Mechanism: This mechanism was hypothesized by both Hargrave and Burns (1979) and Lau (1979) and states that, for a given trap aspect ratio, the degree of water motion at the trap bottom increases with increasing R_t. Lau's experimental study demonstrated this effect. As long as the shear stress on the trap bottom was large enough to resuspend particles, then ϕ_b would increase with increasing R_t. For the mass balance given here (see eq. 2.6 in Section 2.4.1), if ϕ_b increased with increasing R_t, then E would decrease.

The hypothesis stated in this section stipulates that E would decrease only over "some range" of increasing R_t. While Lau's (1979) results (see Figure 2.6) support a flow velocity on the trap bottom dependent on H/D and R_t, these two parameters are not the only parameters that determine when resuspension would occur. As

discussed in Section 2.3.3, a measure of the ratio of critical entrainment stress to resisting force is required to determine the values of stress at the trap bottom for which particles of certain sizes and densities will be resuspended. This is analogous to the sediment transport problem of sediment resuspension where the Shields' curve (Shields 1936) was empirically derived, providing critical erosion velocities for resuspending uniform, noncohesive sediments from a flat bed. This hypothesis addresses only resuspension of particles from the trap bottom. For a particle to leave the trap it must be entrained by the flow within the trap, moved upward to the mouth and then removed from the trap.

Trap Wall Surface Area Effect: This mechanism involves the adhesion of particles to the inside walls of a trap either by electrostatic forces or by chemical adhesion. Particles adhering to the trap wall would result in a decrease in the mass of particles than can be carried out by the flow (e.g., a decrease in C_tQ in eq. 2.3). If particle adhesion is effective only when trap-induced turbulence is low, then a relatively larger amount of material would adhere to the walls at low R_t than at high R_t. At relatively high R_t, high turbulence would potentially disallow adhesion and thus C_tQ would relatively increase and E would relatively decrease. The possibility of particle adhesion on trap walls has never been investigated experimentally and is likely to be a function of the nature of the particles collected, the particle concentration and the nature of the material used to construct the traps, as well as a function of the flow parameters.

Aggregation Model: This model suggests that efficiency differences at different R_t are due to trap-induced particle aggregation. Aggregated particles inside traps have higher fall velocities than individual particles outside traps so relatively more mass can fall to the trap bottom than can fall an equivalent distance in the outside flow. Aggregation depends on the rate at which particles collide and also on the probability that they adhere to one another. Collision rates depend on differential settling, fluid shear and the residence time of the flow in the trap. Cohesion between particles after collision depends on mineralogy, sizes and the quantity and type of cations present. The probability of cohesion can be quantified only through experiments. The disaggregation of particles depends on fluid shear and on collisions between particles with sufficient relative translation energy (Spielman 1978).

It is difficult to predict if the increased shear inside of traps at higher R_t would enhance aggregation or disaggregate particles. However, at higher R_t, the residence time of the flow in a trap does decrease and thus the time for aggregation to occur decreases. Thus, the relative particle collection efficiencies of the traps would decrease at higher R_t.

For this model particles are assumed to aggregate by a shear-controlled mechanism (this and other aggregation mechanisms are described and evaluated in McCave, in press). The R_t-dependence of the aggregation processes and the effect on collection efficiency are summarized as follows. The water outside a trap contains particles

with fall velocity, W. The fluid in the trap is replaced by eddy motion at an average interval t_f (the residence time of the fluid inside a trap). If, over one residence period, shear-controlled aggregation can increase W significantly (by creating larger particles), then the particles inside the trap can fall the distance of the trap faster than they can fall this distance in the flow outside the trap. Thus, $C_tQ < C_oQ$ and all traps, for which aggregation is significantly, are overcollectors (see eq. 2.3). However, if t_f decreases with increasing R_t, then the aggregation process would have less time to operate and the relative difference between C_t and C_o would also decrease. Thus, particle collection efficiencies would decrease for increasing R_t. This mechanism is described in more detail below.

The time (t_c) for particles of a monodisperse (particles all of one size) suspension to aggregate by shear collision (assuming 100 percent efficiency) is

$$t_c = \frac{\rho_p}{C_p} t_s \tag{2.8}$$

where ρ_p = particle density, C_p = particle concentration and t_s = shear time scale; also, note that $C_p/\rho_p = N_c d^3$ (see Section 2.2). For turbulent flows the time scale of the smallest eddies is given by the Kolmogorov microscale, $t_s \simeq (\nu/\varepsilon)^{1/2}$, where ε is the rate of turbulent dissipation. The dissipation rate is difficult to estimate, but is known to be proportional to V^3/L, by virtue of the relationship between the large and small scale turbulence and where V and L are the overall velocity and length

scales of the flow within the trap.

To roughly estimate the magnitude of t_c, it is assumed that ρ_p = 2 g/cm^3 and C_p = 10 mg/l (these are approximately the conditions for the flume experiments conducted in Chapter Three). To estimate the turbulent dissipation rate, V is assumed to be 15 cm/sec and L = 2 cm (approximately the smallest trap diameter tested in the present study, see Table 3.1). For these values, ε = 1700 cm^2/sec^3, t_s = 0.0024 sec and t_c = 480 sec or about 8 min. Thus, for this example, aggregation by shear collision will significantly affect particle fall velocities if the residence time, t_f, is a significant fraction of 8 min. The weaknesses to these estimates are that, (1) ε may be underestimated because the trap may locally increase ε; this would reduce t_s, and (2) t_c may be overestimated because a monodisperse solution was assumed. Both of these limitations would decrease the value of t_c.

To evaluate t_f, assuming that Reynolds number effects are absent, then $t_f \sim L/V$ and

$$\frac{t_f}{t_c} \sim \sqrt{\frac{VL}{\nu}} \left(\frac{C_p}{\rho_p}\right). \tag{2.9}$$

Equation 2.9 states that if t_f does not depend on R_t, then the ratio t_f/t_c will increase because of the effect of R_t on t_c (ε increases at higher R_t and, thus, t_c decreases). For this case, the effect of shear-controlled particle aggregation would increase with increasing R_t, a trend opposite to the predicted effect.

However, t_f may be a strong function of R_t at the transition to turbulent flow. In this case $t_f = f(R_t)\, L/V$ so

$$\frac{t_f}{t_c} = f(R_t)\sqrt{\frac{VL}{\nu}}\,\frac{C_p}{\rho_p} \tag{2.10}$$

If $f(R_t)$ decreases faster than $\sqrt{R_t}$, then the t_f may decrease faster than t_c and shear-controlled aggregation would be more important at lower R_t. Thus, particle collection efficiencies would decrease with increasing R_t. Clearly, it is necessary to experimentally determine the relationship between t_f, t_c and R_t.

The foregoing analysis assumed that the shearing forces, which increase with increasing R_t, would enhance particle aggregation. However, it has been experimentally demonstrated that particle aggregation increases with increasing shear only to a certain threshold shear value and then the shear acts to disaggregate particles (Spielman 1978). The range of shear values that would enhance aggregation or disaggregate particles must be determined for the particle mixture in question. However, it is interesting to note that if, for the range of R_t under investigation, increasing shear enhances disaggregation, then t_f/t_c would increase with increasing R_t. Thus, collection efficiencies would decrease with increasing R_t.

Eddy Model: The eddy model hypothesizes that, if particle concentrations in the fluid removed from a trap in eddies are higher than the particle concentrations in the fluid entering the trap, then E should decrease with increasing R_t due to an increase in the eddy

shedding frequency at higher R_t. It is possible to show that (1) most particles of interest in the ocean can be trapped in the eddy which forms at the trap mouth if they are present when the eddy forms, and (2) that these trapped particles are retained in that eddy for time periods that are long relative to the trap eddy shedding frequency. (A summary of relevant research is provided below.) Thus, when the eddy is shed from a trap, the particles contained in the eddy are shed with it. However, particle concentrations in the oncoming flow and vertical gradients in particle concentration either in the oncoming flow or in a trap have never been measured during calibration experiments. Thus, the hypothesized eddy model remains to be experimentally tested.

The presence of an eddy over the mouth of a trap placed in moving fluid is well-documented (e.g., Peck 1972; Gardner 1977, 1980a; Lau 1979; and the present study in Figures 3.35 through 3.41). Both analytical and experimental studies have provided a reasonably accurate picture of the behavior of a particle in an idealized two-dimensional solid body vortex so that particle orbits and velocities can be calculated. These studies have demonstrated, for a wide range of particle sizes and densities, that particles <u>can</u> remain in the eddy for time periods that are long relative to the shedding frequency. In addition, particle kinematics associated with the eddy motion are important to most of the mechanisms described above. Thus, the behavior of particles within an eddy of general importance to understanding particle exchange and mass balances (e.g., eq. 2.3) within a trap.

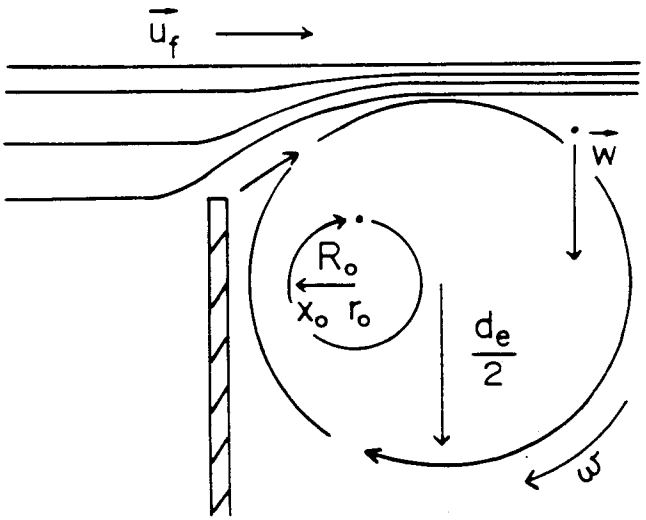
The eddy characteristics and the ability of an eddy to trap and retain particles does clearly depend on R_t. However, as previously stated, for this R_t-dependence on the eddy behavior to result in an R_t-dependence in trapping efficiency, a corresponding change must occur in particle concentration across the trap mouth, either from above or below. From arguments concerning the motion of a particle in a vortex alone, it is not possible to create such concentration differences even through particle retention by an eddy and the time scale for this retention are dependent on the values of both R_t and W relative to the fluid free stream velocity. Thus, in order for the eddy mechanism to be a feasible candidate to explain the observed dependence of collection efficiency on R_t, some other mechanism(s) must be responsible for the required concentration changes. While it is possible to hypothesize a variety of mechanisms by which concentration gradients could be produced, only empirical and experimental studies can elucidate the viability of this proposed eddy model for decreasing E with increasing R_t. A simple model describing particle motion in an eddy is now described.

An eddy is a unique accelerating flow region because the flow can travel through a complete circle. At some point the instantaneous fluid velocity, $\vec{u}_f(t)$, will operate in the same direction as W, enhancing the vertical distance a particle falls, per unit time. Thus, a particle could potentially "fall out" of an eddy. Conversely, a particle could be permanently entrained in the eddy. Conditions for these two limits of particle behavior in an eddy are evaluated here.

In two dimensions, an eddy can be viewed as an idealized

potential vortex. Experimental and theoretical studies have shown that the core region of an eddy behaves essentially like a rotating solid body (Dosanjh et al. 1962; Lamb 1932) where the velocity profile varies as r, the eddy radius. Outside of this core region the eddy behaves like a potential vortex where frictional effects are negligible; here the velocity profile varies as 1/r. Experimental observations of the trajectories of particles (for $R_p \sim 10^{-2}$) inside a horizontal cylinder of rotating fluid (Tooby et al., 1977) provide information on particle behavior, at least in the core region (i.e., the region of solid body rotation), of an eddy.

For an eddy with angular velocity, ω, and for a particle falling at W (refer to Figure 2.10 for the following discussion), the particle will be entrained at a point, x_o, inside the eddy and will then orbit around a point, r_o, lying on a horizontal plane through the center of the vortex, but offset from the center (Tooby et al., 1977). The point was observed to be where the fluid velocity was equal and opposite to the fall velocity (for Stokes particles) or where $r_o = W/\omega$. Because the fluid velocity operates in a direction opposite to fall velocity only on the upstream side of the eddy, particles that remain in eddies are concentrated on the upstream side. The period of the particle orbit is similar to the period of the eddy rotation, but the particle orbits around a radius, $R_o = (x_o - r_o)$. To zero order, the particle inertia can be considered negligible as was done in the general analyses of particle behavior in accelerating flows (presented in Appendix I) and the particle completes a closed loop. However, Tooby et al.'s experimental observations suggest that



$\vec{u}_f$ = fluid velocity

d_e = eddy diameter

ω = eddy angular velocity

$\vec{w}$ = particle fall velocity

r_o = center of particle orbit (w/ω)

x_o = point where particle enters eddy

R_o = radius of particle orbit $(x_o - r_o)$

Figure 2.10: Diagram of particle behavior inside an eddy rotating as a solid core, from the study of Tooby et al. (1977).

particles can slowly change their trajectories in the eddy due to a small inertia force. Thus, eddies may constitute a unique accelerating flow region where particle inertia is important.

A particle will be retained in an eddy only if the particle passes through a region where the core velocity, $r_0\omega > W$. By conservation of momentum, the maximum value for $r_0\omega$ is u_f, the fluid velocity driving the eddy (see Figure 2.10). To determine the maximum fall velocity of a particle that would complete a full orbit inside an eddy, the limits of the eddy diameter must be considered. At the trap mouth, the eddy diameter cannot exceed the inside trap diameter. Thus, for a trap 8.5 cm in diameter (the most common inside mouth diameter of traps used in this study, see Table 3.1), the maximum x_0 for a particle is 4.25 cm. For the particle to complete an orbit entirely within the eddy, R_0 can be a maximum of $x_0/2$ or 2.12 cm. Because r_0 also is 2.12 cm and ω is 2.35/sec (for u_f = 10 cm/sec, r = 4.25 cm), practically speaking, W cannot exceed 5 cm/sec for a particle to be entrained by and complete an orbit within an eddy. Thus, all particles of concern in the present study (see Section 2.4.1 and Section 3.4.2) would be entrained by and orbit entirely within an eddy.

Tooby et al. (1977) observed that particles do not remain in perfectly circular orbits, but some particles spiral slowly inward while other particles spiral slowly outward. When particles left the orbit, they did so on the side with the highest opposed velocity. The empirical relationship which determines inward- versus

outward-spiralling of particles is described by two dimensionless ratios: d/d_e and ρ_p/ρ_f, where d_e = eddy diameter (defined by Tooby et al. as the diameter of the rotating solid core of fluid). For a given particle and eddy size (d/d_e = constant), increasing ρ_p leads to outward-spiralling particle orbits because of the increased centrifugal force on the particle. For a given density ratio (ρ_p/ρ_f = constant), decreasing the particle size or increasing the eddy size leads to outward-spiralling particle orbits. This is because the outside "wall" in solid body rotation confers both drag and lift stabilizing forces to the particle. Thus, the farther the particle is from the wall, the less the particle can benefit from these forces and the greater the tendency for the particle to become unstable and spiral outward.

Based on Tooby et al.'s approximate results, estimates can be made of the maximum particle size (for spheres) which would outwardly spiral for realistic combinations of d_e, d, ρ_p and ρ_f (using d_e = trap diameter, the maximum eddy size to be shed into a trap) for ocean environments (Table 2.5), it is clear that most particles would spiral outward in eddies. For example, all quartz particles with diameters < 0.375 cm will spiral outward in eddies $\leq$ 15 cm in diameter (the range of trap diameters tested in the present study, see Table 3.1). For "low density" particles (e.g., fecal pellets where $\rho_p \simeq 1.20$ g/cm^3, see Taghon et al., in press) the maximum size for an outward spiral is 0.180 cm for eddies shed into the traps tested in this study. Again, the particles of concern in the present study are within these limits. A more detailed model of the behavior

TABLE 2.5

Maximum Diameters of Spherical Particles that would tend to Spiral Slowly Outward, once Entrained in Eddies of Various Sizes

Maximum[1] d_e (cm)	Maximum particle diameter (cm) for quartz grains[2]	Maximum particle diameter (cm) for "low-density particles"[3]
5	0.125	0.060
15	0.375	0.180
25	0.625	0.270
50	1.250	0.600
140	3.500	1.680

1. This is considered to be the inside mouth diameter of a trap
2. $\rho_p \simeq 2.65$ g/cm^3
3. $\rho_p \simeq 1.20$ g/cm^3, e.g., for fecal pellets of the polychaete worm, Amphicteis schaphobranchiatus Moore (Taghon et al., in press)

of a particle in a 2-D vortex which predicts the actual particle orbits as a function of time has been suggested by Nielsen (1979).

The relationship of these observations on particle behavior in an eddy to R_t-dependence of particle collection efficiencies of traps is now reiterated. The major points of the previous discussion of particle (for Stokes' particles only) behavior in an eddy that are relevant to this model are summarized here. (1) Particles initially present when the eddy forms can be retained in the eddy if $\omega r > W$. All particles of interest in this study meet this criteria. (2) Particles in eddies orbit around a point $r_o = \omega/W$, that lies on a horizontal plane through the center of the eddy, but upstream of the eddy center (see Figure 2.10). Thus, particles tend to concentrate within the eddy on the upstream side of an eddy. (3) Although the initial particle orbits are nearly closed, for the particles of interest here, because of a finite inertial force the orbits evolve in time and become unstable so the particles spiral slowly outward. When particles leave an orbit, they do so on the side of an eddy with the highest opposed velocity or the upstream side. (4) Eddies shed behind any vertical barrier are unsteady; for some frequency that is long, relative to the rotational frequency of the eddy (the limit frequency is $\omega = u_f/R$), an eddy is shed and a new eddy is formed.

If the particles stay in the eddy they will be removed from the trap when the eddy is shed. The eddy shedding frequency increases with increasing R_t. However, this mechanism results in a decrease in trapping efficiency with increasing Reynolds number only if the

flux out of the trap is greater than the flux back in.

An additional mechanism which may operate is turbulent mixing near the trap mouth. If the particles are concentrated along the trap mouth due to initial concentration differences or as the unsteady eddy motion moves them up and down, the particles may be mixed upward into the external flow (along the gradient) which then carries the particles horizontally past the trap opening before they can fall back down. Because of the increased concentration on the upstream edge of the trap opening, the concentration leaving is larger than the concentration entering the trap and a decrease in efficiency will result. Because turbulent mixing increases with increasing R_t, a relative decrease in efficiency will occur at higher R_t.

To demonstrate the feasibility of a net particle flux leaving the trap when an eddy is shed, it must be shown that the escape time for particles retained in an eddy is long relative to the frequency of eddy shedding and that this time is long relative to the time for equilibrium to be set up for entrainment into and settling out of the eddy. The magnitudes of the following processes also must be experimentally evaluated for the eddy model to be a feasible mechanism for influencing trapping efficiency. (1) It must be shown that a significant particle concentration gradient develops in an upstream/downstream orientation across the trap. Because particle inertia is responsible for this phenomenon, larger concentration differences are expected in air than in water (where particle inertia

is large relative to fluid accelerations, see Appendix I, eq. AI.4: all μ_f terms are two orders of magnitude smaller in air than in water). Thus, Tauber's (1974) wind-tunnel results are most easily explained by this eddy model. It is interesting to note, however, that u_f/W were of the same order of magnitude in Tauber's study in air and in Peck's (1972) study in water (see Table 2.1) and R_t-dependence on particle collection efficiencies was observed in both studies (see Section 2.3.1). (2) A significant increase in the eddy shedding frequency must be demonstrated for the range of R_t over which particle collection efficiencies decreased.

2.4.3 Particle collection efficiency should decrease over some range of decreasing particle fall velocity

This hypothesis is also supported primarily by the results of Tauber (1974) and Peck (1972) (see Section 2.4.2). The fall velocity dependence on collection efficiency is also suggested by the experimental observations of Tooby et al. (1977). Particles are not retained in eddies unless $r_0\omega > W$, so particles with smaller fall velocities are captured at lower flow velocities. Because particles retained in eddies can leave the trap when the eddy exits the trap, particles with relatively low fall velocities would be caught less efficiently than particles with relatively high fall velocities (i.e., those particles not entrained in eddies). For some range of relatively fast-falling particles (where $W > r_0 w$), eddies would not affect particle trajectories so the particles would not be retained in the eddies. Based on flow observations using dye, Peck (1972) also suggested that, in eddies, denser particles would tend to move

outward, across the lines of flow while relatively lighter particles would tend to move inward or travel with the flow, but no theoretical basis for this prediction was given. The range of fall velocities over which this phenomenon would occur depends on $r_0\omega$.

A relationship between particle fall velocity and collection efficiency was originally suggested in the dimensional analysis (Section 2.2) by the parameter u_f/W. The ratio u_f/W indicates the magnitude of the horizontal component of fluid motion relative to vertical particle motion (gravitational fall velocity). These two terms determine particle trajectories in steady flows and also in unsteady flows if the particles accelerate nearly instantaneously with the flow (see Appendix I). For relatively large values of u_f/W, particles can be displaced or advected, by the flow, for large horizontal distances before the particles can fall any substantial vertical distance. For relatively low values of u_f/w, particles can fall through the flow with minimal horizontal displacement.

One physical mechanism relating the two variables in u_f/W is the dynamics of particle capture by eddies, discussed above, since $r_0\omega$ cannot exceed u_f. Another physical mechanism that may involve the ratio u_f/W is particle aggregation. For a given particle density and shape, fall velocity decreases with decreasing size ($W \alpha d^2$ for Stokes particles). The time scale over which shear-controlled aggregation occurs is shorter for larger-diameter particles than for smaller-diameter particles in monodisperse solutions having the same particle concentrations (McCave, in

press). Thus, if this mechanism is important, at a given R_t the ratio t_f/t_c (see eq. 2.10) would be greater for larger-diameter particles (and, thus, particles with larger W) than for smaller-diameter particles, so the particle collection efficiency would also be greater for the larger particles.

The dependence of a fluid velocity to particle velocity ratio on particle collection efficiency is also suggested by eq. 2.6, for resuspension effects. Here, the velocity ratio ϕ_b/C_oW is, in part, responsible for the magnitude of the resuspension term. As W decreases ϕ_b/C_oW increases so collection efficiency would decrease, due just to resuspension.

The u_f/W ratios that could be calculated in the studies of Peck (1972) and Tauber (1974) (see Section 2.3.2 and Table 2.1) indicate a range for which particle collection efficiencies may be a function of particle fall velocity. These ratios ranged from 9.7×10^3 to 4.1×10^4; for a 10 cm/sec flow (the approximate flow speed during the flume experiments conducted in this study, see Section 3.3.3, and within the range of flow speeds during the field study, see Section 4.3.3) these ratios correspond to particle fall velocities of 2×10^{-4} to 1×10^{-3} cm/sec. Quartz particles falling at these speeds would be < 3.9 μm in diameter or in the "clay" range of natural sediments.

2.4.4 <u>At a given trap Reynolds number, particle collection efficiency should increase over some range of increasing trap aspect ratio</u>

The study of Lau (1979) indirectly supports this hypothesis

because he showed that at a given R_t, the degree of water motion in the bottom of a trap is relatively greater for lower trap aspect ratios than for higher trap aspect ratios; however, he did not determine these effects on particle collection efficiencies. Results of the particle trapping study of Hargrave and Burns (1979) also support this hypotheses, but their data are complicated by the fact that R_t also decreased with increasing aspect ratio (see Section 2.3.3). Hargrave and Burns (1979) also theoretically predicted, by dimensional analysis, that water motion in the bottom of a trap should be a function of trap aspect ratio. In addition, the dimensional analysis conducted here (Section 2.2) predicted that collection efficiency would be a function of aspect ratio.

Resuspension of sediment in the bottom of a trap may result from the increased water motion at the trap bottom (depending on the critical erosion stress of the particles); resuspension would increase the value of ϕ_r relative to C_oW (see eq. 2.6). Thus, the mass of particles carried out of a trap would be greater than the mass of particles carried into a trap. For a given R_t, as aspect ratio increases, water motion at the bottom of a trap would decrease (e.g., the results of Lau 1979) until some asymptotic value of particle collection efficiency is reached; at this asymptotic value, increasing the trap aspect ratio would no longer effect increases in collection efficiency (in other words, the two parameters then would be independent).

Several authors (e.g., Soutar et al., 1977; Hargrave and Burns 1979; Gardner 1980a; Honjo et al., 1980) have suggested that

inserting baffles into the mouth openings of traps would decrease the depth inside the trap for which significant water motion and, thus, resuspension would occur. Baffling would supposedly offset resuspension effects so that baffled traps with relatively low aspect ratios would have collection efficiencies similar to unbaffled traps with aspect ratios at or greater than the asymptotic value of particle collection efficiency. Another requirement was that the aspect ratios of individual cells in the baffle must be in the range of aspect ratios at the asymptotic value of particle collection efficiency. In fact, baffling a cylinder of aspect ratio ~ 4.0 significantly increased its collection efficiency at an R_t of $3.0x10^3$ in the study of Hargrave and Burns (1979) (see Figure 2.8) and Gardner (1980a) found that baffled funnels had higher collection efficiencies than unbaffled funnels (see Figure 2.7).

The range of aspect ratios, for a given R_t, for which resuspension is negligible must be determined experimentally. As previously discussed (in Section 2.3.3), the available data from the calibration studies to date are difficult to interpret because experiments to separate the effect of aspect ratio versus R_t on particle collection efficiency were not conducted. In addition, Lau's (1979) results cannot be applied to these studies because he tested both higher aspect ratios and higher R_t than were tested in the calibration studies (see Figure 2.6).

2.4.5 Effects of trap geometry on particle collection efficiency

The two demonstrated effects of trap geometry on particle collection efficiency are that, relative to cylinders with the same

mouth diameter, small-mouth wide-body traps have higher collection efficiencies and funnel traps have lower collection efficiencies (results from the studies of Gardner 1980a and Hargrave and Burns 1979, see Section 2.3.4). The theoretical treatments of both Hargrave and Burns (1979) and Bloesch and Burns (1980) predicted that, for particle collection efficiencies that are normalized by A_m, efficiencies of traps where $A_m \neq A_b$ could be accounted for by the relationship $C_t = C_o A_m / A_b$, because $C_o W A_m = C_t W A_b$. C_t would be greater than C_o inside traps where $A_m > A_b$ (funnel traps) and C_t would be less than C_o inside traps where $A_m < A_b$ (small-mouth wide-body traps). In calm water C_o enters the trap only by direct settling of particles, but in moving fluid C_o enters the trap also in the volume flux of fluid (Q) and C_t exits the trap in Q (see eq. 2.3). Thus, compared to the situation where $C_t = C_o$, if $C_t > C_o$ the trap will be a relative undercollector and if $C_t < C_o$, the trap will be a relative overcollector (also see eq. 2.7). Theoretically, then, <u>for steady flows</u>, normalizing collection efficiencies by A_b instead of by A_m would accurately represent the true flux of particulates.

Such corrections to the data generally support this prediction (see Table 2.3). Funnel traps tested by Hargrave and Burns and Gardner became relative overcollectors when corrections are normalized by A_b and most of the small-mouth wide-body traps became relative undercollectors after corrections; however, a couple small-mouth wide-body traps were still overcollectors, after corrections (see Table 2.3). These results suggest that the contents

of the entire trap were not well-flushed and the actual area over which particles fall, even in steady flows, is somewhere between A_m and A_b, depending on the trap geometry.

Another physical mechanism to explain funnel-trap collections involves the increased frictional drag of the funnel surface on the flow. For a cylindrical trap, the horizontal solid surface initially encountered by the flow is just the thickness of the cylinder walls. For a funnel trap, the flow tends to follow the funnel contours, dipping into the funnel at the downstream edge of the trap mouth and circulating through the funnel to the upstream edge (see photographs in Figure 3.40). This large surface area would impart more frictional drag to the flow and, thus, relatively more particles may be retained on the funnel surface. In several studies (Gardner 1980a; Hargrave and Burns 1979; and the present study, Section 3.3.6) it was observed that 50 to 70 percent of the material collected in a funnel trap is collected on the funnel. (In the present study, if this material was added to the total flux of particles into the funnel trap body, the trap had a similar collection efficiency to a cylinder.) In a cylindrical trap the flow also dips into the trap mouth at the downstream edge, but the flow circulates throughout the whole cylinder and then to the upstream edge of the trap mouth, so the cylinder walls would also impart drag to the flow. However, an important distinction is that the particles would have a greater distance to fall before reaching a horizontal surface (the trap bottom) in the cylinder and the particles could be re-entrained or retained in the eddy as they fall.

2.5 Summary

In this section the physics of collecting particulates in various designs of traps was theoretically analyzed. A dimensional analysis of most variables relevant to the processes of trapping particulates (Section 2.2) indicated that particle collection efficiency should be a function of primarily three dimensionless parameters, $DV/\nu = R_t$, u_f/W, and D/H, and of trap geometry. The dimensional analysis indicated only that a relationship between collection efficiency and the parameters may exist, for some range of conditions. The dimensional analysis does not indicate the nature of the dependence. Thus, for a first approximation of how the dimensionless parameters may quantitatively effect particle collection efficiency, results from the five published laboratory studies (Peck 1972; Tauber 1974; Gardner 1980a; Hargrave and Burns 1979; Lau 1979) that investigated trap collection characteristics were summarized, relative to the dimensionless parameters (Section 2.3). From this summary of observed trap biases, three hypotheses were developed regarding biased particle collections by cylinders (presented in Sections 2.4.2, 2.4.3, and 2.4.4) and two hypotheses were developed regarding the relationship of collection efficiency to trap geometry (see Section 2.4.5). These hypotheses were supported by theoretical arguments or models and serve as guidelines for selecting trap designs to be flume-tested in the present study, for the purposes of testing the biological hypothesis central to this thesis.

From this analysis it is clear that characteristics of particle

collecting traps require rigorous investigation in the future. The laboratory studies, to date, provide a valuable groundwork for future experiments but must be evaluated in light of their limitations. Future experiments might be fruitfully organized by testing the hypotheses presented in Section 2.4. In addition, it is emphasized that laboratory experiments must be carefully designed so that (1) competing physical effects are minimized (i.e., R_t must be constant when aspect ratio effects are being tested and visa versa), and (2) dynamic and geometric similarity to the field is achieved (i.e., R_t and particle characteristics, especially W, must be matched).

3. LABORATORY MEASUREMENTS OF LARVAL FALL VELOCITIES AND OF PARTICLE COLLECTION EFFICIENCIES FOR SEVERAL TRAP DESIGNS

3.1 Introduction

The experimental design for testing the hypothesis that larvae act like passive particles in flows near the seabed involves using the biased sampling characteristics of sediment traps. A theoretical analysis of trap biases, based on observations from the literature, was presented in Chapter Two. Results of this analysis indicated that particle collection efficiencies of a single trap design may vary significantly over a range of flows and particle types; in addition, for a given flow regime and particle type, collection efficiencies are expected to vary between certain trap designs. Thus, traps must be calibrated for the specific field environment in which they will be deployed and for the specific particle types that will be collected.

In this chapter, results are presented from laboratory measurements to determine fall velocities of nonswimming polychaete larvae and to determine relative particle collection efficiencies of a variety of sediment trap designs. Fall velocities of larvae were measured directly by allowing the organisms to sink through a temperature-controlled column of water. The traps were calibrated in a laboratory flume using particles with fall velocities similar to the measured larval fall velocities and using a flow speed within the range of flow speeds measured at the field study site (see Section 4.3.3).

The primary purpose of the flume study was to find trap designs with significantly different relative particle collection efficiencies (e.g., a pair of trap designs where one trap design significantly overcollects particles relative to the other). The traps then could be used in field experiments with the a priori hypothesis that the rank order of collections by the different trap designs will be the same for passively falling larvae in the field and for passively falling inert particles (with fall velocities similar to larvae) in the flume. Only flume results for the traps actually deployed in the field to test this hypothesis are presented in Chapter Three.

A second purpose of the flume study was to experimentally test some of the predictions from the theoretical analysis of particle trapping (Chapter Two). In particular, the prediction that particle collection efficiency of straight-sided cylinders should decrease with increasing trap Reynolds number (R_t) was tested. Also tested was the effect on particle trapping of trap aspect ratio (the ratio of the height to the inside mouth diameter of a trap) and of placing honeycomb baffles in traps with various aspect ratios. Results of these flume experiments are presented and discussed in Appendix II.

3.1.1 Unique requirements for trap calibrations in the present study

It was necessary to do a flume study for selecting traps to use in the field because previous published laboratory flume studies calibrating a variety of trap designs (Gardner 1977, 1980a; Hargrave and Burns 1979) were not conducted at trap Reynolds numbers large

enough to be applicable to conditions at the chosen field site in the present study. Field experiments, planned in the present study, were to be carried out at a shallow subtidal (15-m depth) station in Buzzards Bay, MA (see Section 4.1.2). At this site flow speeds 0.5- and 1.0-m above the seabed can vary between 0 and 22 cm/sec daily because the currents are primarily tidal (a full description of the physical measurements taken at the study site is given in Section 4.3.3). For experiments conducted at the study site during the summer of 1980, 8.5 cm was the minimum trap mouth diameter that yielded enough larvae of a single species to permit meaningful statistical analyses of samples for short-term ($\leq$ 5 days) deployments. Assuming that the kinematic water viscosity (ν) is 1.185×10^{-2} cm^2/sec for seawater at atmospheric pressure, 20° Centigrade (C) and a salinity of 30 parts per thousand (ppt), R_t could vary between 0 and 1.9×10^4 in flows at the study site. In the studies of Gardner (1977, 1980a) and Hargrave and Burns (1979) calibrations for a variety of trap designs were done only for R_t between 4.0×10^2 and 5.1×10^3 (see Table 2.1 and Figure 2.1). Studies of pollen collection by traps (Peck 1972; Tauber 1974) were conducted at R_t up to 9.9×10^4 (see Table 2.1 and Figure 2.1); however, only a single trap design, the "Tauber trap" (diagramed on Figure 2.2), was tested in these studies.

A new set of trap calibrations also was necessary in the present study because of the nature of the particles (falling invertebrate larvae) to be collected. In the flume studies of Gardner (1977, 1980a) and Hargrave and Burns (1979) natural sediments composed of a

variety of particle sizes, with fall velocities varying over several orders of magnitude, were used during trap tests. Gardner (1977, 1980a) used abyssal mud from the North American basin which was sieved to remove particles > 63 μm (median grain diameter = 2.6 μm, 95 percent of this material was < 25 μm, as determined by Coulter Counter analysis). For these natural sediments, particle fall velocities theoretically could vary by at least four orders of magnitude; from Stokes equation (Stokes, 1851) for spherical quartz (ρ_p = 2.65 g/cm^3) particles falling through freshwater (at atmospheric pressure and 20°C), a 62.5-μm particle falls at 3.5×10^{-1} cm/sec, a 22.1-μm particle at 4.4×10^{-2} cm/sec, a 2.76-μm particle at 6.8×10^{-4} cm/sec, and a 0.98-μm particle at 8.6×10^{-5} cm/sec. Particles used by Hargrave and Burns (1979) potentially cover even a larger range of fall velocities because natural sediments from Bedford Basin were sieved to remove only particles > 125 μm.

Because the theoretical analysis (Chapter Two) indicated that trap collection efficiency may be sensitive to particle fall velocity, it was desirable to conduct the present flume study using, (1) particles with fall velocities similar to those measured for falling invertebrate larvae and, (2) that these particle fall velocities varied over as narrow a range as possible (preferably, less than one order of magnitude).

3.1.2 Design criteria for calibrations of traps in a laboratory flume

Flume calibrations of sediment traps, like any test of a model, must be conducted so that conditions during collections

in the laboratory are "geometrically" and "dynamically" similar to conditions during use of the prototype (full-scale traps) in the field. Geometric similarity is satisfied if traps used in the laboratory and in the field have identical relative dimensions (e.g., aspect ratios), form, and texture. Dynamic similarity between laboratory and field flows around traps is maintained if trap Reynolds numbers and particle fall velocities are similar between the flows (see Section 2.2). In addition, there are a variety of aspects to the flume design and to the procedures for conducting the flume experiments which must be carefully considered to minimize experimental error. Each of these aspects to the flume experiments are outlined below. Specific considerations for designing the flume and conducting the experiments in the present study are discussed later in this Chapter (Section 3.2). Some of the design and operation criteria outlined below have not been carefully considered in previous laboratory calibrations of sediment traps (e.g., see Section 2.3.5).

A. Characteristics of the Oncoming Flow Field: Important characteristics of the oncoming flow field during particle trapping in the field must be simulated in the laboratory. It is necessary here to clearly distinguish between the flow Reynolds number (R_f, characterizing the oncoming flow field) and the trap Reynolds number (R_t, characterizing the flow near the trap mouth). Maintaining similar R_t between laboratory and field flows indicates that flows near the trap mouth have similar hydrodynamic characteristics (e.g., turbulence). However, the R_t does not necessarily reflect the

characteristics of the oncoming flow field because both the characterisitic velocity and length scales for R_t may differ considerably from these characteristic scales for R_f.

To illustrate the differences between R_t and R_f in field and in flume experiments, I will work through an example using a cylindrical trap 30-cm tall with a 10-cm diameter mouth collecting in field and laboratory flows that are 10 cm/sec at the height of the trap mouth. The characteristic velocity scale for the R_t is defined as the mean stream velocity at the height of the trap mouth; the characteristic length scale is the trap dimension normal to the flow (usually analogous to the outside diameter at the trap mouth). Assuming that the kinematic water viscosity is of the order 10^{-2} cm^2/sec in all calculations, then R_t for traps in both field and laboratory flows is of the order 10^4. Characteristic length and velocity scales for R_f are defined differently depending on the physical process driving the flow and on the flow environment. For this example, I use locally depth-limited boundary layers in both the flume and the field, the field flow driven primarily by the tides. For these flows, the characteristic length scales of R_f for both the flume and the field are defined as the water depth; the characteristic velocity scales are the depth-integrated velocities. For simiplicity in this example, I also assume that the depth-integrated velocites in both flume and field flows closely approximate the velocity of 10 cm/sec, at the trap mouth. Thus, water depth determines the magnitude of the difference between $R_{f\text{-field}}$, $R_{f\text{-flume}}$, and R_t. In the flume a water depth of the order 10^2 cm

is reasonable for this size of trap (see "Boundary-Layer and Free-Surface Effects", discussed below) so $R_{f\text{-flume}}$ is of the order 10^5. In the field, a depth-limited tidally driven boundary layer exists at the field site (15-m depth) chosen for the present study, where flows of 10 cm/sec at the height of the trap mouth are common. A water depth of the order 10^3 cm makes $R_{f\text{-field}}$ of the order 10^6.

This example illustrates that achieving dynamic similarity between R_t in field and laboratory experiments does not indicate that dynamic similarity also exists between $R_{f\text{-field}}$ and $R_{f\text{-flume}}$, characterizing the hydrodynamic nature of the oncoming flow fields. With the velocity scale and kinematic water viscosity held constant for calculations of R_f and R_t in this example, R_t is two orders of magnitude smaller than R_f; $R_{f\text{-field}}$ and $R_{f\text{-flume}}$ differ by an order of magnitude. This example also indicates the difficulty in attempting to match R_f between field and laboratory flows. Because water depth is the only variable in calculations for this example, a flume water depth of the order 10^3 cm would be necessary to achieve dynamic similarity between $R_{f\text{-field}}$ and $R_{f\text{-flume}}$ if full scale traps are to be tested in the flume. A flume of this size is infeasible. Alternatively, increasing the depth-integrated flume flow speed by an order of magnitude would make $R_{f\text{-flume}}$ of the same order as $R_{f\text{-field}}$; however, this would require decreasing the dimensions of model traps tested in the flume by an order of magnitude (trap mouth diameter would then be 1 cm) to maintain similarity between $R_{t\text{-field}}$ and $R_{t\text{-flume}}$. Other scaling problems then may arise because of changes in the ratio of particle fall

velocity to trap mouth diameter between the flume and the field.

In some cases, achieving similarity between $R_{f\text{-field}}$ and $R_{f\text{-flume}}$ may even be misleading because, (1) the nature of the flow regime is also a function of the roughness scale of the bottom boundary, and (2) there are a variety of techniques for "dampening" or "tripping" turbulence in a flume. For example, a low Reynolds number for the flume flow (of the order 10^2) may be "tripped" into turbulent flow in the flume by inserting a barrier of small vertical projections sticking above the seabed. Likewise, large eddies in a turbulent flume flow can be "dampened" by various baffling techniques. Clearly, achieving dynamic similarity between laboratory and field R_f is a difficult, and sometimes impossible, task. However, it is unnecessary to have exact similarity between $R_{f\text{-field}}$ and $R_{f\text{-flume}}$ as long as the hydrodynamic characteristics important to trap dynamics in the respective oncoming flow fields are similar.

It is especially important that turbulence in a field flow be mimicked in the laboratory because particle displacement in turbulent flows is distinct from particle displacement in laminar flows. In laminar flows, particle paths can be predicted from flow measurements (e.g., mean velocity profiles). The horizontal component of the mean particle trajectories is determined by the flow streamlines (lines of constant horizontal velocity) and the vertical component by the particle fall velocity. Almost all particles in water have so little inertia that they accelerate almost instantaneously with the flow (see Appendix I) and thus tend to follow flow streamlines exactly. In turbulent flows, particles are constantly mixed both vertically

and horizontally by the chaotic motions of turbulent eddies. The eddies actually have a vertical velocity component acting in the direction opposite to particle fall velocity. The positions of particles in turbulent flows cannot be predicted from flow measurements (such as mean velocity profiles) because all velocity terms also contain random fluctuating components. Thus, in a turbulent flow regime particles are potentially well-mixed in the water column, but in laminar flows particles segregate by fall velocity; the availability of particles to be collected by traps clearly will differ in turbulent and laminar flow regimes.

In summary, important hydrodynamic characteristics of the oncoming flow field during trap collections cannot be determined from the trap Reynolds number (R_t) of the flow. A separate calculation is necessary to determine the flow Reynolds number (R_f). The magnitude of $R_{f\text{-field}}$ is required for determining if traps are collecting in a turbulent or in a laminar flow field. Exact similarity between $R_{f\text{-field}}$ and $R_{f\text{-flume}}$ is not required; however, it is essential that traps collecting in turbulent field flows are also collecting in turbulent flume flows (and, likewise, for laminar field flows). The hydrodynamic nature of flume flows are not necessarily indicated by $R_{f\text{-flume}}$ because flows can be manipulated to "dampen" or "trip" turbulence. Thus, flume flow characterisitics should be determined directly by detailed velocity measurements and from dye studies. Insuring similarity between important dynamic aspects of the oncoming flow regimes in field and laboratory flows indicates that particle mixing and, thus, particle

availability to traps in the two environments will be similar.

B. Boundary-Layer and Free-Surface Effects: Flume experiments must be carefully designed so that the boundary-layers of fluid forming on the side walls, bottom and top (if there is no free-surface) of the flume do not interfere with trap collections. If the flume is not completely enclosed, exposing a free-surface of water to the air, then trap mouths must be carefully positioned at a depth below the water surface where interaction with the free surface is minimal. These boundary-layer and free-surface effects must be minimized because they are experimental artifacts of confining water flow to a small enclosed area relative to the aerial extent of enclosed fluid flow in the field.

As fluid flows past a boundary (or "wall") the frictional (viscous) forces of the boundary on the fluid result in a velocity gradient increasing away from the wall. The velocity of the fluid precisely adjacent to the wall equals zero and at the top of the frictional layer the flow reaches the "mean stream velocity" (where there is no longer a detectable boundary effect of friction on the flow speed). The region of strong velocity gradient and frictional influence is called the "boundary layer." The region where the flow has reached its mean stream velocity is called the "potential" or "frictionless" region of the flow. Boundary layers are associated with <u>all</u> surfaces placed in moving fluid. In steady uniform flows the boundary-layer thickness (perpendicular to the surface) depends on the flow speed and on the horizontal distance from the leading edge, the form of the leading edge and the roughness of the surface.

For boundary-layer considerations, two ways flume experiments can be designed are given here. (1) Traps are placed in the region above the boundary layer. In this case, the location of the test section and the dimensions and placement of traps in this section are stipulated by the boundary-layer thicknesses on all walls of the flume. The test section is usually placed as close to the flow source as possible so that boundary-layer growth is minimized. Boundary-layer thicknesses can be calculated from equations for growth of laminar or turbulent boundary layers over various surfaces. Detailed velocity measurements and flow visualization techniques can be used to directly estimate boundary-layer thicknesses. (2) Traps are placed entirely within the boundary-layer region of flow. In this case, the bottom boundary layer is allowed to grow over the entire water column, or in flows completely enclosed on all sides, boundary layers on all walls are allowed to grow together into a "plug" flow. This option is necessary when it is impractical to place the test section close enough to the flow source to limit boundary layer growth. For example, the flow may require "straightening" (e.g., the flume flow in the present study, see Section 3.2.4) or other manipulations to prevent secondary circulation so that the test section must be moved downstream. When traps are collecting inside the bottom boundary layer of free-surface flume flows, it is desirable to select a region of flow where the vertical gradient of horizontal velocity is small.

Because traps are usually deployed well below the water surface in the field, it is also important to eliminate possible free-surface effects in the laboratory. Depending on the nature of the flume

flow, waves may propagate along the free-surface. In addition, air currents in the room may add to free surface water motion. In most cases, the depth below the surface required to minimize possible free-surface effects for various flows has not been determined empirically. However, these depths can be roughly estimated by equations for flow around an obstacle or by observing the water surface when a trap is moved vertically from the flume bottom up through the water column until a water surface disturbance is detected, due only to the presence of the trap. During experiments, the trap mouth then should be placed well below this water depth.

There are three effects of the trap on the flow which also must be considered in the flume design. (1) Boundary layers develop over all trap surfaces exposed to the flow. (2) The flow must accelerate to go around a trap; thus the flow streamlines are distorted (curved) until some distance away from the trap where the flow is restored to the mean stream velocity (and streamlines are, again, parallel to the bed in laminar flow). (3) The trap acts as a solid body restricting the cross-sectional area of the flume; thus, to conserve mass, the flow speed must locally increase on the sides, above and below the trap. The implications of these effects for designing flume experiments on particle trapping are discussed in the succeeding three paragraphs.

The thicknesses of boundary layers forming on trap surfaces are usually small because trap dimensions are not large enough to allow significant boundary layer growth in the downstream direction. However, in flows with characteristically thick boundary layers

(e.g., laminar flows), experiments must be designed so that trap boundary layers are not allowed to interact with flume boundary layers or boundary layers on other traps.

Displacement of flow streamlines by a trap could result in secondary circulation effects in the flume if curved streamlines of flow hit and are deflected by the flume walls. The flow speeds up as it moves around a trap, according to Bernoulli's principle. As the flow encounters the trap the flow speed drops to zero at the front of the trap (called the "stagnation point") and, for a cylinder, the maximum velocity increase (and thus, the maximum streamline curvature) occurs at a 90° angle on a horizontal plane from the stagnation point. Using potential flow theory (that is, neglecting streamline displacement due to the trap boundary layer) and ignoring circulation, it can be shown that the accelerated velocity 90° from the stagnation point on a cylindrical trap is still about 10 percent greater than the mean stream velocity at distances of three trap radii to either side of the cylinder. Thus, to avoid possible problems of trap-induced secondary circulation in the flume, experiments should be designed so that a distance of at least three trap radii lies between the trap and the flume walls.

A local increase in flow speed due to significant blockage of the cross-sectional flume area by a trap especially would be a problem if several traps, arranged in upstream/downstream arrays, are tested simultaneously. In this case, the downstream distance required for the flow to recover to its original flow speed must be determined and the traps positioned accordingly. This will also

insure that downstream traps are not collecting particles in a complicated flow wake created from boundary layer formation on and streamline displacement by upstream traps. Errors in estimating trap Reynolds numbers may also result if flow speeds are significantly increased over the trap mouths due to cross-stream blockage of flow. Thus, experiments should be designed so that cross-sectional trap area is small relative to the flume cross-sectional area to minimize blockage of flow.

C. Choice of Particles for Seeding Flume Flow: The kinds of particles used in flume trapping experiments should be carefully selected to represent the particles that will be collected by traps in the field. Particle fall velocity is the most important particle characteristic to match between laboratory and flume flows (see Sections 2.2 and 2.4.3). If particles in the seeded flow cover a narrow range of fall velocities (e.g., less than an order of magnitude), then it may be unnecessary to monitor the fall velocity spectrum of particles collected by traps (but see also Sections 3.4.4 and 3.4.5). However, because biased trapping may be a function of particle fall velocity, when particles covering a wide range of fall velocities are used to seed the flow, the fall velocity spectrum of particles actually collected by traps must be determined (e.g., by calculating Stokes' fall velocities from Coulter Counter analyses of particle size distributions in samples).

Another important consideration in particle selection is possible particle/particle interactions due to aggregation processes. Particles carefully selected to represent a specific

range of particle fall velocities may, in fact, settle faster in flume flows if the particles aggregate. Aggregation is a function of particle size, the surface charge on the particle, the fluid characteristics, the flow regime, particle concentration, and turbulent flow characteristics (see Section 2.4.2).

A discussion of the physical processes controlling particle aggregation (Brownian motion, laminar and turbulent shear, turbulent inertial coagulation, differential settling, and biogenic aggregation processes) for ocean environments is provided in the recent review of McCave (in press). McCave also calculated the rates of aggregation and the size ranges of particles most affected by the different processes. These predictions may serve as guidelines for selecting particle sizes and particle concentrations to use in flume experiments. However, because characteristics of the particle surface (e.g., electrical charge) are often difficult to predict, it is also important to confirm in situ particle fall velocities during flume experiments. If particles are large (> 100 μm), fall velocities of particles in suspensions taken from the flume can be estimated directly in a particle settling chamber (e.g., see Sections 3.2.2 and 3.2.3). The extent of aggregation also can be detected from the size spectrum of particles collected in flume water samples. Note, however, that most techniques for sizing particles involve the use of a particle dispersant (e.g., Calgon for dispersing clays in pipette analyses of natural sediments). Techniques for sizing particles must be appropriately modified (e.g., not using Calgon) so that natural particle interactions in the flume are not destroyed

during analyses of water samples.

D. Measurements During Flume Experiments: Several guidelines, discussed below, for taking measurements during flume experiments will improve the precision of collection efficiency estimates for a single trap design. Increasing measurement precision increases the probability of detecting statistically significant differences between collections by different trap designs (e.g., lower α-levels can be used if experiment-wise variability is low). It is essential to test replicates of each trap design to determine within-trap variability. If this variability is inherently high, then more replicates may be required to decrease the probability that a false null hypothesis will be accepted (that is, to decrease the β-error of the experiment).

Prior to experiments, the flume flow should be carefully studied to uncover dead spaces, areas of backflow or other peculiar circulation patterns. Ideally, detailed velocity profiles should be made at several points across the flume channel upstream and downstream of the test section. If an accurate current meter that averages velocities over very small distances (e.g., a laser-Doppler velocimeter or a hot-wire anemometer) is unavailable, then dye studies or other flow visualization techniques can be used to qualitatively estimate the nature of the flume flow. The flow regime and the location of the test section then can be modified to meet the criteria discussed in (A) and (B) above.

During experiments, flow speed measurements at the height of the trap mouth are necessary for accurately estimating trap Reynolds numbers. The flow speed at the height of the trap mouth can be

calculated from velocity measurements taken elsewhere in the water column (e.g., at the water surface) only if the vertical structure of the profile of horizontal velocities is known. At a given flow speed, placing all trap mouths at the same height above the flume bottom insures that all traps experience the same local flow regime and also simplifies measurements of flow speed.

Trap "particle collection efficiency" is defined as the "actual particle collection" by the trap divided by the "predicted particle collection" for an unbiased collector. In previous flume studies of trap collection efficiencies, a variety of methods have been used to determine the predicted particle collection. All methods assumed that the trap mouth presents a flat horizontal surface to the flow into which particles can settle. Estimating the number or weight of particles available to settle on this surface is done by sampling the water column or sampling the flume bottom for particle concentration. Note, however, that the trap mouth presents a flat surface to the flow at some distance above the bed. The technique for seeding the flow with particles, the spectrum of particle fall velocities and the mixing of particles in the flume water column determine the similarity between material deposited on the bottom and material deposited on a flat surface some distance above the bottom. For example, heavy particles may fall below the height of the trap mouth before the water mass reaches the trap. These particles are unavailable for collection by the trap and should not be included in estimates of particle concentration used to calculate predicted particle collection. Sampling the flume bottom in front of the trap

would, in this case, give an erroneous estimate of particle availability.

It is critical that the distribution of particles in the flume water column be carefully monitored during the course of trapping experiments. Conditions should be adjusted to insure that the water mass sampled, for estimates of predicted particle collection, represents the particles available in the water mass actually encountered by the trap mouth. A well-mixed water column sampled slightly upstream of the test section at the height of the trap mouth is probably the best safeguard against biased estimates of particle concentration. The ideal technique for sampling the water column depends on the nature of the flume flow regime and the particles to be collected. Calibrations of the technique are required to determine possible biases (e.g., see Section 3.2.5, for water column sampling technique used in the present study).

3.2 Materials and Methods

3.2.1 Measurements of larval fall velocities

Fall velocities of nonswimming polychaete larvae were determined by allowing anesthetized or freshly killed organisms to sink through a temperature-controlled column of water (hereafter referred to as a "settling chamber"). Initially the measurements were made in a settling chamber (referred to as the "large chamber") designed by Dr. Arthur R.M. Nowell using larvae collected from near-surface waters adjacent to Friday Harbor Laboratories (F.H.L.), San Juan Island, WA. Based on results of these measurements, Nowell's large

chamber was scaled down and modified for later fall velocity measurements conducted at the Coastal Research Laboratory (C.R.L.), W.H.O.I., using larvae reared in the laboratory. The modified settling chamber at W.H.O.I. is referred to as the "small chamber." The two settling chambers, procedures for making measurements in each chamber and the larvae used for fall velocity estimates are described below.

3.2.2 Measurements in the large chamber

The large chamber consists of a cylindrical glass tube (wall thickness = 1.6 mm, inside diameter = 9.5 cm, total height = 122 cm) surrounded by a Plexiglas cylinder (wall thickness = 6.5 mm, inside diameter = 18.9 cm). The outside cylinder extends 4-cm above the inside cylinder and serves as a water bath; particles and organisms were allowed to sink through the inside water column. Plexiglas struts fix the inside cylinder equidistant from all walls of the outside cylinder. The entire periphery of the inside cylinder is permanently etched with a thin line 2-cm above the bottom and lines 0.5-m and 1.0-m above it. The two cylinders are attached at the bottom to a glass funnel fitted with a glass and Teflon stopcock to allow retrieval of settled items (particles or larvae). The entire apparatus is mounted on a 16- by 30- by 30-cm Plexiglas base.

The inside cylinder was filled with glass-fiber filtered water from the seawater system at F.H.L. Each time the water was replaced in the settling chamber, water salinity was determined to ± 0.1 ppt from measurements of the specific gravity and temperature of the water; the seawater was always 31.0 ± 0.5 ppt. Nozzles located near

the bottom and 8-cm below the top of the outside cylinder permit connection with a temperature-control unit or a seawater system. For fall velocity measurements in the present study, the seawater system at F.H.L. was connected by flexible tubing to the bottom of the cylinder, the water exiting the cylinder through tubing at the top. A continuous flow of water through the outside cylinder maintained the water temperature of the inside cylinder within 1°C of ambient seawater temperature. Particles in the water circulating through the outside cylinder often prohibited detection of the particle or larva sinking through the inside water column, so the incoming water was filtered using several kinds of in-line automobile fuel filters. To further restrict particle contamination of the water columns, a clear glass plate covered them whenever possible.

To facilitate location of particles and larvae settling through the chamber, all fall velocity measurements were done in a dark room with an incandescent light mounted above and shining directly down through the inside chamber. To minimize warming of water in the top of the cylinders, this light was turned on only during the period of time that an organism or particle was falling (hereafter called a "run"). Even so, a temperature gradient in the water columns always developed over time, the water at the top of the chamber being 0.1 to 0.5°C warmer than the water at the bottom. Thus, water temperature at the top, middle and bottom of the inside water column was measured before and after each run.

Prior to measurements of larval fall velocities, the precision of fall velocity estimates in this settling chamber was determined

for a variety of inert particles. Two types of spherical particles were selected to cover the range of fall velocities expected for larvae: glass spheres (Ferro Class IVA "Uni-spheres", Cataloque No. 608, claimed by Ferro to contain $\leq$ 15 percent irregularly shaped particles) with a particle density (ρ_p) of 2.42 g/cm^3, and red plastic spheres of an unknown origin, but the vial containing these spheres was labeled as ρ_p = 1.06 g/cm^3. In addition, the fall velocities of two types of nonspherical particles were measured: natural quartz sand grains, dried and presieved to a specified size range ($\rho_p \simeq 2.65$ g/cm^3), and fresh fecal pellets of the clam, Macoma balthica (Linnaeus), discoid in shape (ρ_p unknown). Methods for making fall velocity measurements (e.g., the method of introducing the particle into the water column) were adjusted to minimize the coefficient of variation (CV) for replicate runs of the same particle.

Larvae were collected by towing a 250-μm plankton net through near-surface waters adjacent to F.H.L. The samples were maintained in the running seawater table at F.H.L. and live polychaetes sorted under a dissecting microscope. Prior to the run, each larva was essentially narcotized to death (see below).

Trial and error experiments were conducted using various concentrations of the anesthetizing agents, magnesium chloride ($MgCl_2 \cdot 6 H_2O$, hereafter referred to as "$MgCl_2$"), tricaine methanesulfonate (sold under the brand name "Finquel" by Ayerst Laboratories and hereafter referred to as "MS222"), chlorobutanol (Parke, Davis and Co., hereafter referred to as "Chloretone"), and KCl. These experiments indicated that the chemical concentrations

and immersion times required to maintain a larva in a nonswimming status for its entire fall through the water column, usually killed the larva. Larvae would not revive in fresh seawater following these treatments. It is unclear when actual physiological death took place in each individual. The resultant accuracy and precision of fall velocity estimates is discussed later (Section 3.4.1). Some larvae were not anesthetized, but were killed directly, using formalin, ethanol, or freshwater and then settled in the chamber. These treatments were designed to be "worst case" estimates of the true nonswimming fall velocities of living larvae; formalin is a tissue fixative and would be expected to increase the density of the organism, ethanol is a drying agent and may decrease the organism's density, and freshwater would be expected to make the organism neutrally buoyant. The precise treatments (chemical concentrations, duration of treatment, duration of immersion in fresh seawater, and total elapsed time before a run) for each fall velocity measurement are given in the results (Section 3.3.2).

Using an occular micrometer in a dissecting microscope, treated (nonswimming) larvae were measured usually at 70X prior to a run. Measurements of length (hereafter referred to as the "narcotized length") and width (hereafter referred to as the "narcotized width") were made on each individual in its narcotized, or otherwise treated, configuration (see Figure 3.1). These measurements represent the maximum and minimum cross-sectional distances presented by a sinking larva to the water during its fall. The total number of setigers also was estimated, when possible. Other notes were made regarding

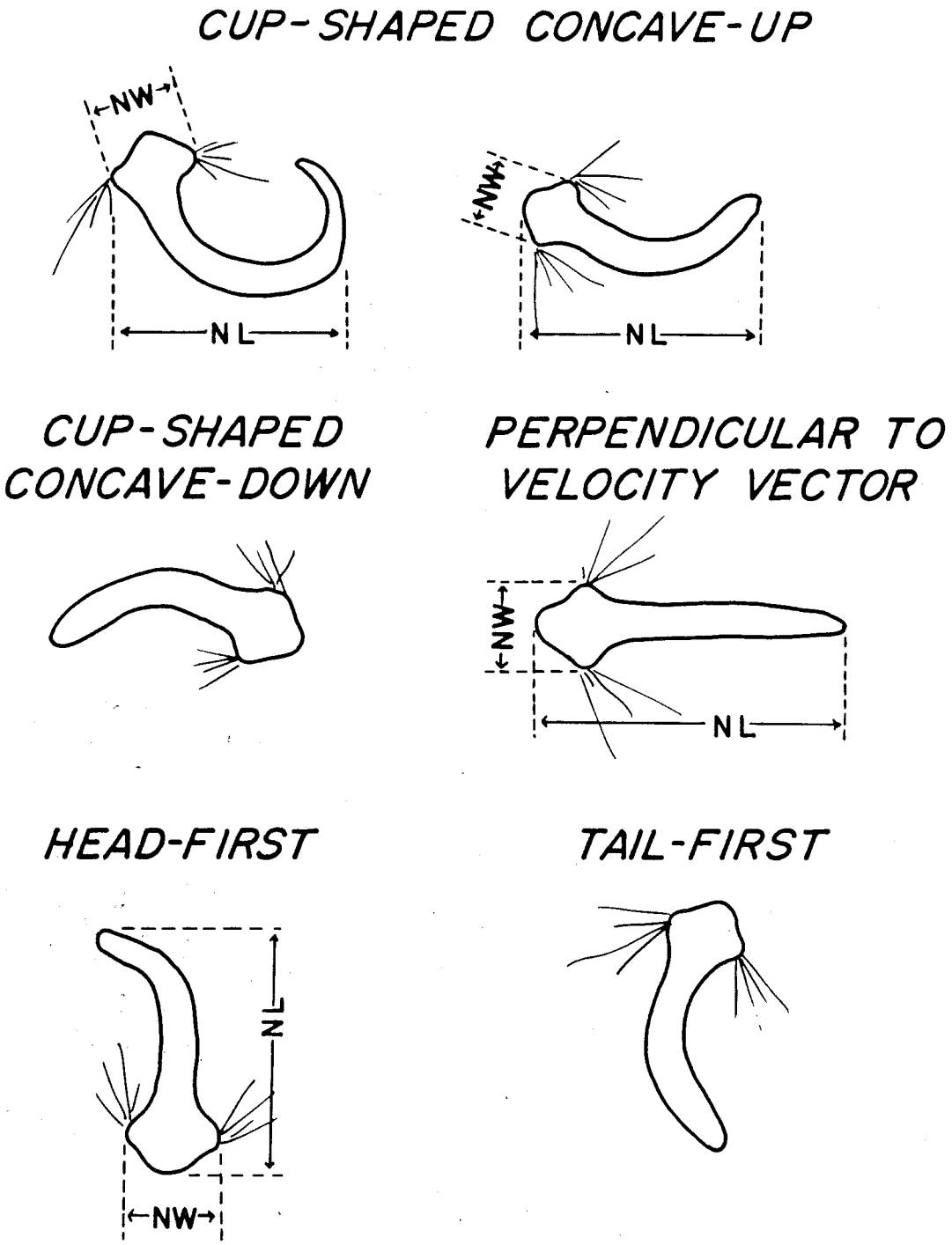


Figure 3.1: Diagrams of nonswimming polychaete larvae showing where the "narcotized length" (NL) and "narcotized width" (NW) was measured on each individual, prior to a run. The common orientations of the larvae, as they fell through the water columns, are labeled above the diagrams.

the orientation of the setae on treated larvae, the stickiness of and amount of particulate matter clinging to a larva and the degree to which an individual curled after treatment (e.g., see Figure 3.1).

For a run, first the water temperature (to ± 0.1°C) in the center of the inside cylinder was measured at the bottom etched line and the 0.5-m and 1.0-m marks above this line. Then the room lights were switched off and the light above the chamber was switched on. A larva was carefully introduced into the water using a micropipette. The technique involved manipulating the organism into a drop of water at the tip of the pipette and then gently pushing this drop below the water surface. The amount of forward momentum and other peculiar motions incidentally conferred to the organism upon introduction was judged by the author; if the organism had not hydrodynamically "recovered" from the introduction by the time it reached the mark 1.0-m above the bottom, the organism was retrieved and introduced again. The elapsed time for an organism to fall from the 1.0-m to the 0.5-m mark and from the 0.5-m mark to the bottom mark (also a distance of 0.5 m) was recorded with a stop watch to ± 0.1 sec. After the run, temperatures in the water column were recorded again.

Considerable effort was made to retrieve each individual through the stopcock at the bottom of the chamber. However, sometimes larvae stuck to the sides of the funnel before reaching the stopcock. In addition, because the water in the inside chamber at the funnel was not surrounded by an outside water bath, this water tended to warm faster than the rest of the water column as the room temperature increased during the day. Thus, many of the larvae would reach this

warm water mass and rise, only to sink again as they encountered colder water above; some larvae circulated several cycles in this convection cell. To remedy this problem, three adjustments were made. (1) When possible, fall velocity measurements were taken only during the early morning (0400 to 1000), before the sun began warming the room. (2) When this was not possible, a dish of ice was placed under the funnel to cool the water so a larva's fall velocity would actually increase in this area. (3) Alternatively, the stopcock was opened before a larva reached the funnel's warm water mass to create a current of water carrying the organism down. Whether the funnel water was warmed by the air or cooled by the ice bath, it was impossible to determine how far up into the water column this temperature anamoly permeated. Thus, only fall velocity estimates made in the top 0.5 m (between the 1.0-m and the 0.5-m marks) of the water column are presented in the results.

3.2.3 Measurements in the small chamber

The large chamber was not originally designed for determining the sinking rates of low-density particles or live organisms, but for estimating the fall velocities in seawater of inert particles that sink relatively fast (e.g., sands, with fall velocities of the order 10^{-1} to 10^{0} cm/sec). During the runs in the large chamber, it became evident that several modifications of the chamber were necessary to improve the measurement precision in fall velocity estimates of larvae. For example, the column of water must be tall enough so that a sinking larva reaches its terminal fall velocity (i.e., it is no longer accelerating) before the measurement interval

(etched onto the inside chamber walls), but the column height also must be adjusted to minimize convection currents and other sources of error (e.g., changes in orientation of the organism) during the fall. As previously mentioned, a convection cell did develop due to differential cooling of water near the bottom of the large chamber. While most sands would fall straight through this cell, larvae were displaced by it because larval fall velocities (of the order 10^{-2} cm/sec, see Section 3.3.2) are less than the water velocities in the convection currents. To reduce the possibility of such differential cooling in the small chamber, the total height of the inside water column was reduced to 35 cm and the outside water bath was designed to surround the bottom as well as the sides of the inside chamber (see Figure 3.2). In addition, lines were etched on the inside chamber at intervals every 5-cm above the bottom so that changes in fall velocity over small distances could be documented (in the large chamber fall velocity estimates were averaged over 50-cm intervals, severely limiting error estimates). The rationale for other aspects to the design of the small chamber are discussed as the chamber is described below.

The small chamber was constructed of Plexiglas (wall thickness = 6.4 mm) using a non-toxic organic glue (ethylene chloride) as a sealant. The inside and outside water columns are square so organisms can be observed and photographed through flat surfaces either macroscopically or with a dissecting microscope mounted on an adjustable vertical rod. The two columns are drawn to scale in Figure 3.2. The outside column can be fitted with nozzles connecting

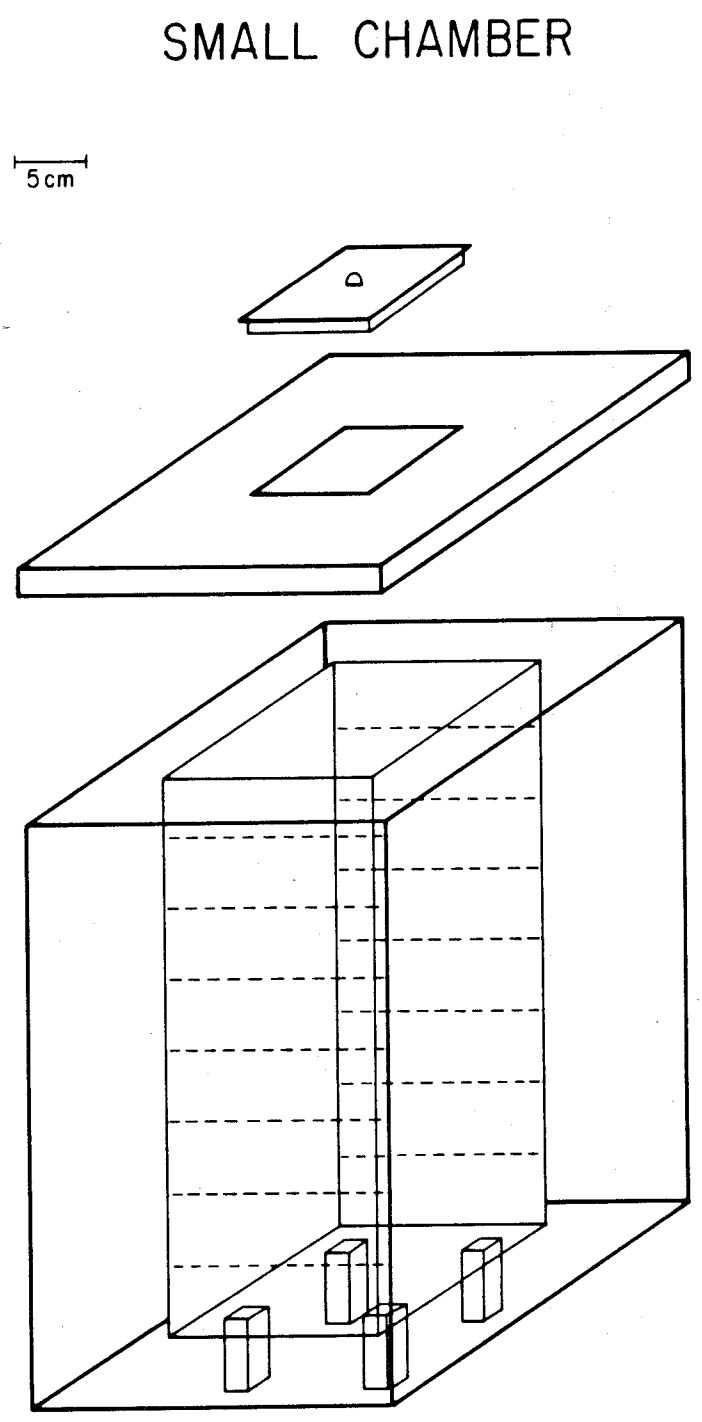


Figure 3.2: Diagram (to scale) of the "small chamber" used for measuring fall velocities of nonswimming polychaete larvae. See text for a full description of this chamber.

hoses to a temperature-control unit or a running seawater system, but this was not necessary in the present study because measurements were conducted in a temperature-controlled (21 ± 1°C) room at the C.R.L., W.H.O.I. A tight-fitting lid covers the chamber at all times to aid in temperature-control and to reduce particle contamination of the column. Only an 8-cm square trap door centered on the lid is removed momentarily to introduce or retrieve organisms.

For measurements, both water columns were filled with filtered (using a 1-μm filter) seawater from the seawater system at the Environmental Systems Laboratory (E.S.L.), W.H.O.I. The water was warmed to room temperature in the E.S.L. system and, once inside the small chamber, allowed to equibrate for several days with the air temperature in the temperature-controlled room at the C.R.L., until air bubbles no longer formed in the water. Organic aggregates developed in the water over time; when these aggregates interferred with observing sinking organisms, the water was changed. For the time period of the fall velocity measurements, January through May 1983, the salinity of the E.S.L. water was ~ 32 ± 0.5 ppt. Although fluctuations in water salinity in the inside column were not monitored directly, the fluctuations are expected to be small because the chamber is tightly sealed to minimize evaporation.

In the small chamber, fall velocities were measured for larvae of the spionid polychaete, Streblospio benedicti Webster, raised in the laboratory by Dr. Lisa A. Levin. This species has a different larval type in the west coast and the east coast populations (L.A. Levin, personal communication). Fall velocities were determined on

larvae reared from west coast adults (collected in Mission Bay, CA) and on larvae reared from east coast adults (collected from the Marine Ecosystems Research Laboratory or MERL Microcosms which were originally filled with benthos from Narragansett Bay, RI; see Grassle et al., 1981). The larvae were chemically treated and measured as previously described for larvae tested in the large chamber (Section 3.2.2). However, following any chemical treatment of a larva, it was placed in fresh, untreated seawater for a period of time before introduction into the settling chamber. This served as a "washing" treatment, a precaution to reduce the possibility that a chemical surface film would remain on the organism during its fall, contributing to inaccuracies in the measurements.

Temperature was measured to 0.1°C at 5-cm intervals throughout the inside water column. Initially, fall velocity measurements were made in a dark room with the falling larva illuminated by an incandescent light positioned 15- to 30-cm above the chamber and shining down through the inside water column. As with measurements in the large chamber, the focused light was turned on only during a run. However, this was long enough to slightly warm the surface water creating a maximum temperature gradient throughout the column of 0.3°C. Unfortunately, a dark room with focused light was necessary in order to see small larvae (ranging from 100 to 300 μm in length) fall through the column. For larger organisms, measurements could be made in a lit room, without the focused light. Still, the surface water in the inside chamber responded to changes in air temperature faster than the bottom water (completely surrounded by a

water bath) so temperature gradients of 0.1 to 0.2°C were often present.

A larva was introduced into the surface water of the inside chamber with a micropipette, as described for measurements in the large chamber (Section 3.2.2). The organism was allowed to fall to the line etched 30-cm above the bottom; the descent of the larva was usually timed for the five 5-cm intervals from 30- to 5-cm above the bottom. Thus, a "vertical profile" of 5-cm averaged fall velocities could be constructed as well as obtaining a 25-cm averaged fall velocity for the entire fall. Once the organism fell below the mark 5-cm above the bottom, it was retrieved from the water with a micropipette. Recovery of individuals was excellent with this technique, facilitating replicate runs of the same organism. Observations of particle movement in the water, after a larva was retrieved, indicated that six minutes were required for the column of water to recover from the disturbance. Thus, runs were always made at least 10-min apart.

The error involved in making fall velocity measurements in the small chamber was determined by runs using spherical plastic beads (Polystyrene Divinylbenzene No. 141 Microspheres, specific gravity = 1.05, from Duke Scientific) having fall velocities within the range of those expected for larvae. Because perfectly spherical particles always present the same cross-sectional surface area to the flow during their fall, runs with these beads yield the minimum amount of measurement error expected for this technique.

3.2.4 Flume design

Collection efficiencies of a variety of trap designs were determined in a freshwater flume located in the Ralph M. Parsons Laboratory for Water Resources and Hydrodynamics at Massachusetts Institute of Technology. The flume consists of a wood basin 945-cm long, 417-cm wide, and 121-cm deep modified for these experiments according to the design criteria outlined previously (Section 3.1.2). A centrifugal pump recirculates water from a sump-section downstream to an upstream diffuser; the flow is unidirectional.

Model tests of traps in the flume were designed for field trap Reynolds numbers ranging from 6.8×10^3 to 1.3×10^4, based on a predicted mean flow speed in the field of 10 cm/sec, trap mouth diameters ranging from 8 to 15 cm, and $\nu = 1.185 \times 10^{-2}$ cm^2/sec (seawater at atmospheric pressure, 20°C, 30 ppt). Modifications to the flume necessary to achieve these trap Reynolds numbers were primarily stipulated by the maximum fluid discharge rate (0.056 m^3/sec) of the pump. This pumping rate provides maximum flow speeds of 1.1 cm/sec over the unmodified basin. To achieve 10-cm/sec laboratory flows, the flume had to be narrowed to ~ 60 cm at the test section and the water depth reduced to ~ 75 cm. In addition, full-scale traps were tested in the flume to maintain trap Reynolds number similarity between laboratory and field flows. Even so, trap Reynolds numbers in the flume were slightly higher (see Appendix III) than predicted for the field because freshwater was used in the flume experiments ($\nu = 0.9136 \times 10^{-2}$ cm^2/sec for freshwater at atmospheric pressure and 24°C).

The rectangular flume basin was modified (for the following description refer to Figure 3.3) by constructing a "raceway" (made of 12.7-mm thick marine plywood) 61-cm wide and 75-cm tall centered in the basin and covering 615 cm of the flume length. To straighten the flow funneled into the raceway, a curved "entrance section" (made of 3.2-mm thick polyethylene plastic) attaches the raceway to the basin walls 79-cm downstream of the diffuser. Just upstream of the sump area, vertical walls connect the raceway to the basin on both sides. These walls could be raised or lowered to allow water behind the raceway when the flume was being filled or to prevent backflow into these "support areas" during experiments. The entire structure was attached to the flume basin with L-brackets, sealed at the bottom with silicone cement and duct tape, and supported on all sides by water. In addition, five 122-cm by 244-cm wood braces were wedged into place on top of and at various distances along the raceway, spanning the flume width. The braces applied the downward force necessary to balance the buoyancy of the wood. All wood in the flume had a smooth finish, either with a resin-based paint or with varnish.

The test section begins 435-cm downstream of the diffuser. Defining the length of the test section is a box (made of 12.7-mm thick marine plywood) 91-cm long, 61-cm wide and 75-cm deep with a glass window (12.7-mm thick) connecting the box to the raceway. Inside the box and leaning at a 45° angle away from the window is a mirror (107-cm wide, 91-cm tall, and 64-mm thick). The box was designed to be water-tight allowing observations and photographs of traps during experiments; the observer perches on a catwalk laid

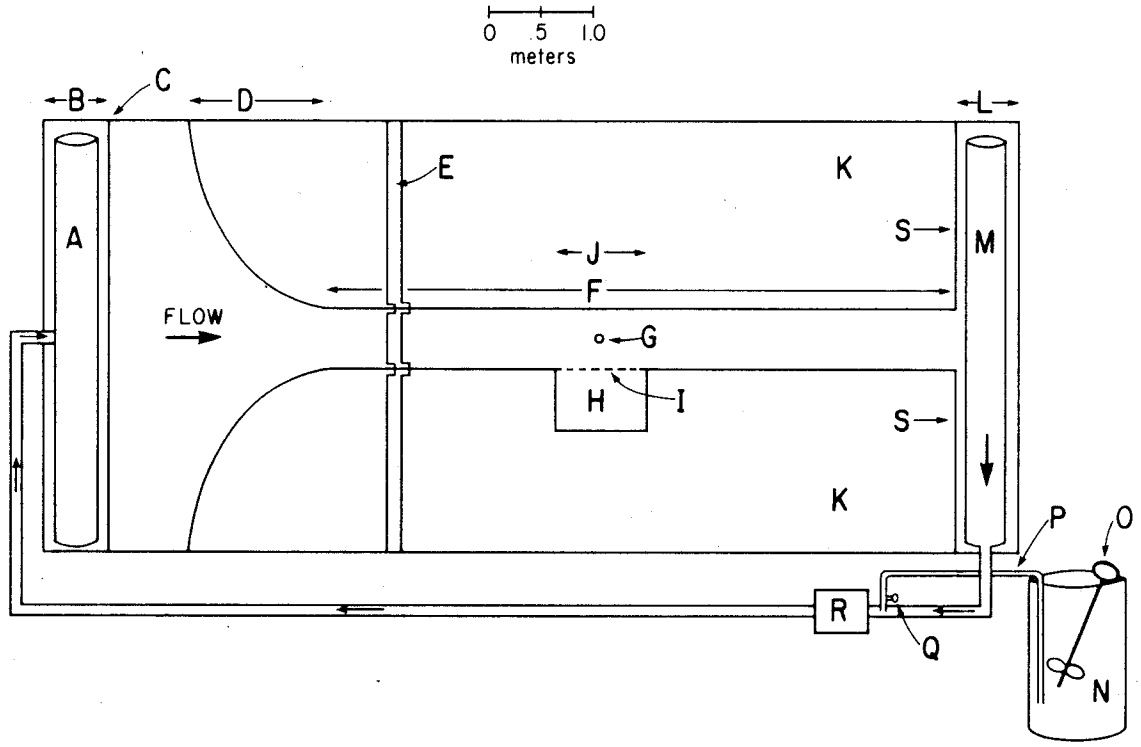


Figure 3.3: Diagram (to scale) of the flume used to measure particle collection efficiencies of traps. The flume is viewed here from above. The following features are referred to in the text: A = diffuser, B = depressed well housing diffuser, C = point where flume basin begins, D = flow-straightening area or entrance section to the raceway, E = one of the five wooden braces supplying a downward force on the raceway, F = raceway, G = threaded flange to hold PVC post and trap (see Figure 3.4), H = dry box holding mirror, I = window, J = test section, K = support areas filled with water during experiments, L = sump area, M = pipe returning flow to centrifugal pump, N = bead tank, O = outboard motor, P = hose connecting bead tank to valve on pipe leading to centrifugal pump, Q = adjustable valve to regulate flow from bead tank, R = centrifugal pump, S = removeable vertical walls to allow water into support areas.

across the flume and looks down on the mirror to observe a trap at the test section.

The location of the test section was selected so that traps would be collecting particles in a unidirectional turbulent flow field with minimal boundary-layer growth. As the flow from the diffuser narrows from spanning a width of 417 cm to a width of 61 cm, peculiar circulation patterns were observed in the curved entrance section and at the mouth of the raceway. Thus, the test section was positioned a sufficient distance downstream to allow restoration of these secondary flows to a unidirectional flow regime. The maximum distance the test section could be moved downstream was limited by the thicknesses of the turbulent boundary layers on the bottom and side-walls of the flume. An accepted formula (e.g., see White 1979, pg. 400) for calculating the turbulent boundary layer thickness, δ, at some downstream distance, x, from the leading edge of a smooth flat plate is

$$\delta \simeq \frac{(0.16)(x)}{(\frac{u\,x}{\nu})^{1/7}} \qquad \text{where } u = \text{mean stream velocity of the flow.}$$

This formula assumes a non-turbulent starting flow; because this clearly was not the case in the present study (see Section 3.3.3), the δ-estimates made here should be considered approximate. The bottom boundary-layer thickness at the trap stand, 481-cm downstream of the basin edge, (i.e., excluding the well housing the diffuser) is 11.7 cm (assuming $\nu = 0.9136 \times 10^{-2}$ cm^2/s for freshwater at atmospheric pressure, 24°C). During flume experiments, trap months

were placed either 34-, 47- or 51-cm above the bottom, well above this bottom boundary layer. Determining the point at which the boundary layer on each flume side wall begins to grow is more difficult. Assuming that the secondary circulation patterns in and before the entrance section interfer with boundary-layer development in this region, then the leading edge for side-wall boundary-layer growth would be the leading edge of the raceway. Thus, the side-wall boundary-layer thickness 273-cm downstream of the raceway entrance is 7.2 cm (assuming the same value for ν used above). For nine of the traps tested in the flume, the side-wall boundary layer is at least three trap radii from the largest diameter of the trap (see last column of Table 3.1). This is probably a sufficient distance so that side-wall boundary-layer interference with trap collections will be negligible (see Criteria B, Section 3.1.2). However, for seven of the trap designs tested, only two trap radii lie between the traps and the side-wall boundary layers. Thus, results of experiments using this latter group of traps were carefully evaluated to determine possible boundary-layer interference with particle trapping.

At maximum pumping rate, the diffuser supplies to the raceway a flow field containing numerous turbulent eddies. The turbulence arises because, (1) the pumping system is not completely water-tight so air bubbles are introduced with the water; the bubbles rise in the upstream section of the flume, mixing the water mass and (2) the diffuser ports point downward but, because the diffuser is depressed in an upstream well (see Figure 3.3), the oncoming flow rebounds off the sides of the well creating a churning and swirling water mass

TABLE 3.1

Trap Dimensions and the Number of Trap Radii Between Each Trap and the Side-Walls or Boundary Layers on the Side-Walls of the Flume

Trap design	Trap code[1]	Wall thickness (cm)	Height (cm)	Inside mouth diameter (cm)	Maximum outside diameter at trap mouth (cm)	Aspect ratio[2]	Average measured trap volume[3] (ml) ()=N	Number of trap radii from each side-wall of flume[4]	Number of trap radii from estimated boundary layer on each side-wall of flume[5]
tenite butyrate cylinder	TBC1.7-3.0	0.1	5.2	1.7	1.9	3.0	13 (6)	31.1	23.5
tenite butyrate cylinder	TBC3.6-3.1	0.1	11.2±0.1	3.6	3.8	3.1	116 (6)	15.0	11.3
tenite butyrate cylinder	TBC7.4-2.9	0.15	21.8±0.1	7.4	7.7	2.9	909 (5)	6.9	5.0
tenite butyrate cylinder	TBC14.7-2.9	0.4	43.9	14.7	15.5	2.9	7179 (6)	2.9	2.0
tenite butyrate cylinder	TBC14.7-1.6	0.4	23.6±0.2	14.7	15.5	1.6	3705 (3)	2.9	2.0
tenite butyrate cylinder with funnel inside	TBF14.7-1.6	0.4	24.0±0.2	14.7	15.5	1.6	3698 (3)	2.9	2.0
opaque plastic cylinder	OPC8.5-1.0	0.1	8.7±0.1	8.5±0.1	8.7	1.0	478 (12)	6.0	4.4
opaque plastic cylinder	OPC8.5-1.9	0.1	16.0±0.1	8.5±0.1	8.7	1.9	939 (11)	6.0	4.4
opaque plastic cylinder with funnel inside	OPF8.5-1.9	0.1	16.0±0.1	8.5±0.1	8.7	1.9	459 (9)	6.0	4.4
opaque plastic cylinder with funnel inside	OPF8.3-1.9	0.1	16.0±0.1	8.3±0.1	8.7	1.9	388 (3)	6.0	4.4

TABLE 3.1 (cont. - 2)

Trap design	Trap code[1]	Wall thickness (cm)	Height (cm)	Inside mouth diameter)cm)	Maximum outside diameter at trap mouth (cm)	Aspect ratio[2]	Average measured trap volume[3] (ml) ()=N	Number of trap radii from each side-wall of flume[4]	Number of trap radii from estimated boundary layer on each side-wall of flume[5]
opaque plastic cylinder	OPC8.5-2.7	0.1	22.8±0.2	8.5±0.1	8.7	2.7	1349 (43)	6.0	4.4
opaque plastic cylinder with plate surrounding mouth	OPP8.3-2.7	0.1	22.9±0.3	8.3±0.1	15.2±0.1	2.7	1457 (3)	3.0	2.1
opaque plastic cylinder	OPC8.5-3.6	0.1	30.2±0.1	8.5±0.1	8.7	3.6	1820 (15)	3.0	4.4
opaque plastic cylinder with funnel on top	OPF14.1-1.6	0.1	22.8±0.2	14.1±0.1	14.5	1.6	1788 (3)	3.3	2.3
opaque plastic gallon jar	OPG8.3-3.0	0.1	24.9±0.1	8.3±0.1	8.5*	3.0	3787 (12)	3.0	2.1
opaque plastic gallon jar with cylinder on top	OPGC8.5-3.6	0.1	30.7±0.1	8.5±0.1	8.7*	3.6	4150 (3)	3.0	2.1

1. Traps will be referred to in the text and in tables and figures by these "trap codes;" the first two letters refer to the material the trap is made of, the letter(s) that immediately follow refer(s) to the trap geometry, the number before the hyphen refers to the inside mouth diameter, and the number following the hyphen refers to the aspect ratio.
2. Ratio of trap height to inside mouth diameter.
3. Actual measured trap volumes are listed in Appendix III.
4. These numbers were calculated for traps centered in a 61-cm wide flume.
5. These numbers were calculated for traps centered in a 61-cm wide flume with 7.2-cm boundary layers on each side-wall (see Section 3.2.4).

* Maximum body diameter = 15.2 cm.

upstream of the entrance section. The flume is not long enough to allow complete dissipation of these eddies downstream. No steps were taken to baffle the flume flow because the flow near (within two meters of) the bottom at the field study site was expected to oscillate between smooth- and rough-turbulent; detailed measurements of velocity profiles made by Dr. William D. Grant at the study site in October of 1982 comfirmed this prediction (W.D. Grant, personal communication). Visualizations of the flume flow using dye showed that the eddies in the flow approaching a trap are small (see Figure 3.17 and Figures 3.35 through 3.41); the flow regime is not dominated by any large-size eddies that may result purely from entrance section secondary-flow phenomena.

Because of the limited size of the test section, only one trap could be placed in the flume at a time (refer to Figure 3.4 for the following description). Each trap was raised above the bottom on a PVC (polyvinyl chloride) pedastal (1.9-mm diameter); the lengths of the pedastals were adjusted so that all trap mouths were raised to approximately (± 0.5 cm) the same height above the bottom, during a given series. The pedastal screwed into a threaded flange (10-cm diameter, 1.4-cm thick) centered in the test section 481-cm downstream of the diffuser well and equidistant from the side walls (see Figure 3.3). Another flange was screwed onto the top of the pedastal and the trap was held vertical in a "basket" made of four stainless steel struts (2.5-cm wide, 1.6-mm thick) fastened by stainless steel bolts to the bottom of the flange. The struts usually extended only about half-way up the height of the trap and never extended above the trap

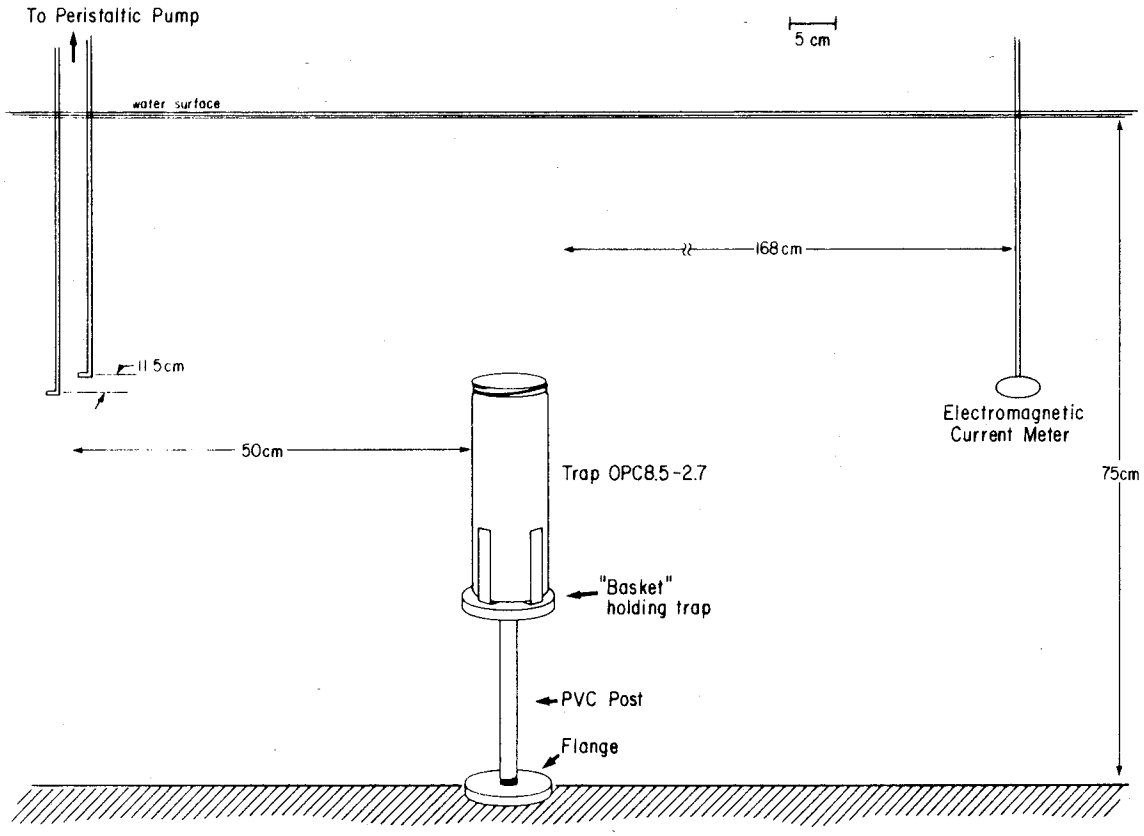


Figure 3.4: Side-view of the flume at the test section showing location of trap in relation to the peristaltic pump water sampling tubes upstream and the electromagnetic current meter downstream. This diagram is drawn to scale and a full description is provided in the text.

mouth. The orientation of a trap during a collection interval could be viewed through the mirror in the box; care was taken to insure that trap mouths were horizontal to the flume bottom (and, thus, to the unidirectional flow) during all collections.

Flow speed was monitored in the water column with an electromagnetic current meter positioned 168-cm downstream of the trap pedastal at the height of the trap mouth (see Figure 3.4). The meter averages current speed over a vertical distance of about 4 cm and is accurate to ± 1 cm/sec. From observing random fluctuations in flow speed during early experiments, it was clear that speeds varied only over a range of 4 cm/sec (from 8 to 12 cm/sec); anamolously high or low speeds never occurred. Because the pump was set at the maximum discharge rate during all experiments, flow speed was monitored in detail only during a few trap collection intervals. In these cases, an observer recorded the flow speed every 10 sec during a given interval. Variability in flow speed resulting from differences in flume water height during and between "series" of flume experiments is discussed later (Section 3.3.3). (A "series" of experiments includes three replicates of all trap designs tested during a single day [a continuous 6- to 10-hr interval].) Detailed velocity profiles were not possible using this current meter because it averages velocities over a large vertical distance (~ 4 cm) relative to the estimated thickness (~ 12 cm, calculated previously) of the bottom boundary layer at the test section, it is accurate only to ± 1 cm/sec, and it is sensitive to the presence of solid boundaries. Thus, dye techniques were used to roughly characterize the flume flow regime.

Photographs of dye streaks various distances above the bottom are presented in Section 3.3.3.

3.2.5 Seeding the flow with glass beads and sampling the water column

The flume was filled with freshwater from the Cambridge City water system. During the fill, the water was filtered through a diotomaceous earth filter. The flume was drained, cleaned, and refilled for each new series. The water was at ambient outside air temperature when it entered the flume, so it warmed considerably during each series. Thus, water temperature was measured (to 0.1°C) in the flume test section, at the height of the trap mouths, approximately every hour during a series.

To limit bacterial action on particles in the flume water, 3.8 liters of bleach (5.25 percent, by weight, of sodium hypochlorite, NaClO) was added to the flume during each fill. This resulted in NaClO concentrations ranging from 0.353 millimolar (mM) for a flume water height of 50 cm (or ~ 7600 liters of water) to 0.235 mM for a flume water height of 75 cm (or ~ 11,400 liters of water).

The flow was seeded with spherical glass beads (Ferro Class IVA "Uni-spheres", claimed by Ferro to contain $\leq$ 15 percent irregularly shaped beads; ρ_p = 2.42 g/cm^3) selected to have fall velocities within the range of those experimentally determined for larvae (see Section 3.3.2). For all series, except one, beads specified by Ferro to be 13 to 44 μm in diameter (Ferro Catalogue No. 3200) were used. Coulter Counter analyses of two bead samples indicated a unimodal distribution of bead diameters; 93.9 to 94.2 percent of the beads

were between 12.7 and 50.8 μm and 84.1 to 85.3 percent were between 16.0 and 40.3 μm (see Figure 3.5A for the frequency distribution of bead sizes). Mean bead diameters of 24.8 and 24.9 μm in these two bead samples were calculated by assigning the frequency of beads in a Coulter Counter size class to the midpoint of that size class, summing over the size classes and determining the average bead diameter. Hereafter, these beads will be referred to as the "25-μm bead mixture." In two series (see Table 3.10), beads specified by Ferro to be 28 to 53 μm in diameter (Ferro Catalogue No. 2740) were used. Coulter Counter analyses of two samples of these beads also indicated a unimodal distribution of bead diameters; 97.4 to 97.8 percent of the beads were between 32.0 and 64.0 μm (see Figure 3.5B). Mean bead diameters (calculated as for the 25-μm beads) for these two samples were 46.5 and 46.4 μm. Hereafter, these beads will be referred to as the "46-μm bead mixture."

The beads were mixed with water in a separate "bead tank" (95.3-cm diameter, 121.9-cm tall, 874.4-liter capacity, see Figure 3.3) by sprinkling preweighed amounts of dry beads onto the water surface. For one series (8/24/82), preweighed lots of the 25-μm bead mixture were sonicated in clean glass jars containing deionized water, several days prior to the series. These sonicated beads, maintained in suspension by manually shaking the jars, were then poured into the bead tank during the course of the series. A homogeneous bead suspension was maintained by continuous mixing with an outboard motor, the rotor extending to a height of 15- to 20-cm above the bottom.

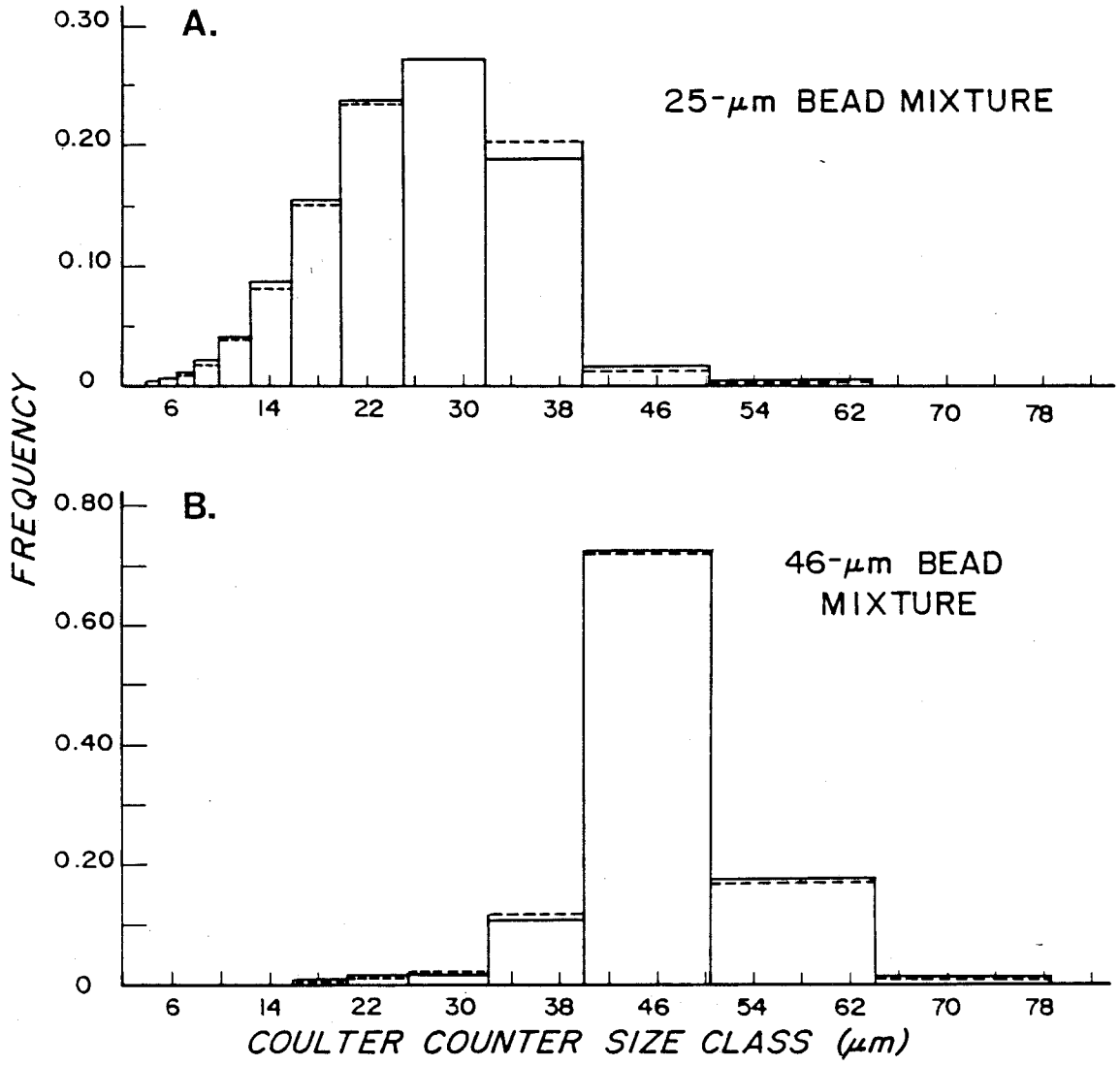


Figure 3.5 Size-frequency histograms of the 25-μm bead mixture (A) and the 46-μm bead mixture (B) used to seed the flume flow. Two samples from each bead mixture were analyzed using a Coulter Counter. The mean bead diameters for each of the four samples were 24.90 μm for the first 25-μm bead sample (dotted line in A), 24.80 μm for the second 25-μm bead sample (solid line in A), 46.35 μm for the first 46-μm bead sample (dotted line in B) and 46.74 μm for the second 46-μm bead sample (solid line in B).

The flume flow was seeded with the bead-tank suspension through an adjustable valve on the pipe leading from the flume into the centrifugal pump (see Figure 3.3); the combined forces of pump suction and the pressure head on the bead tank carried the suspension into the pipe. A manometer on the hose leading from the bead tank into the pipe was used to monitor the supply of beads to the flume. From theoretical calculations of the settling loss rate of beads over the length of the flume and from several "seeding experiments" (where loss-rate was determined directly), it was eventually possible to seed the flow such that flume bead concentrations during trapping experiments were maintained roughly between 8 and 12 mg/l (actual ranges in bead concentrations are given in Table 3.10), with very gradual changes.

A relatively large pressure head on the bead tank was necessary to supply bead suspensions to the flume at the required rates. Thus, for most experiments, the bead tank water level was maintained between 25- and 30-cm above the bottom. The tank was initially filled with water to a height of 30 cm and beads were added to achieve a predetermined concentration. Once the bead tank was drained a vertical distance of 5 cm, it was refilled to the 30-cm level with water and beads, maintaining the original desired concentration. This refill process took about 7 min. Regular gradual oscillations in flume bead concentrations correlated with these refill periods.

Bead concentration during flume experiments was monitored using a peristaltic pump water sampler. A pair of glass tubes (2.5-cm

long, 11.1-mm diameter), separated by 11.5 cm, were positioned on a frame so they were parallel to the flume bottom and faced directly into the flow. Each tube connected to a flexible hose (11.1-mm diameter) leading through one of the two persitaltic pump drums and into a collection jar. The frame holding the tubes was clamped onto a point gauge with a vertically traversing vernier scale and lowered into the water only during sampling, thus minimizing disturbance to the flow during trapping. The tubes were centered equidistant from the flume walls and, for all series except one, the tubes collected water 50-cm upstream of the trap pedastal. In one series (6/7/82), the tubes collected water 10.2-cm upstream of the pedastal.

Water samples to determine bead concentrations during a given trap collection interval were always taken at the height of the trap mouth. In addition, vertical profiles of bead concentrations were made three times during each series (see Section 3.3.3 and Figure 3.19). Discrete water samples were taken as quickly as possible (over 4- to 6-min time periods) at consecutive 10-cm intervals above the bottom. An accurate profile requires simultaneous water samples at each depth. However, because the flow was continuously seeded, particle concentrations at a single depth changed very gradually with time (usually at rates of ~ 0.10 mg/l per min) so that concentrations varied by a maximum of 10 percent over any given 8.5-min interval (see Appendix III). Thus, the variability in concentrations for samples at different water depths and samples at the same water depth should be similar over short time intervals (e.g., 8.5 min).

During the 5/25-5/26/82 series, particle concentrations using

the peristaltic pump sampler were compared with collections using three other water-sampling techniques, to determine the most desirable method for sampling the water column. All methods sampled the water mass 10-cm in front of the trap stand and at the height (34 cm during this series) of the trap mouths; however, traps were not placed in the flume during these comparisons. The three alternative water-sampling methods involved inserting a sampler, initially capped at both ends, into the flume flow by hand. The sampler was oriented so that its mouth faced directly into the flow. To take a sample, the cap on the upstream end of the sampler was removed so that flowing water quickly entered and displaced the air in the sampler; the lid was replaced at depth, before bringing the sampler to the surface. The methods differed only in the size and shape of the samplers: "tenite butyrate cylinders" (7.4-cm inside diameter, 7.6-cm tall, 2-mm wall thickness), "300-ml bottles" (small-mouth wide-body plastic jars with 1.8-cm inside mouth diameter, 6.0-cm maximum body diameter, 13.4-cm tall, and 1.5-mm wall thickness), and "500-ml bottles" (similar in shape to the 300-ml bottles, but with 2.2-cm inside mouth diameter, 7.2-cm maximum body diameter, 16.8-cm tall, and 1.0-mm wall thickness).

From a visual inspection of plots of particle concentrations estimated using all four sampling methods (Figure 3.6), the mean and the within-method variability in estimates of particle concentration for each sampling method appear to be similar. In addition, these estimates do not appear to differ substantially or directionally from the mean and the between-method variability in particle concentration

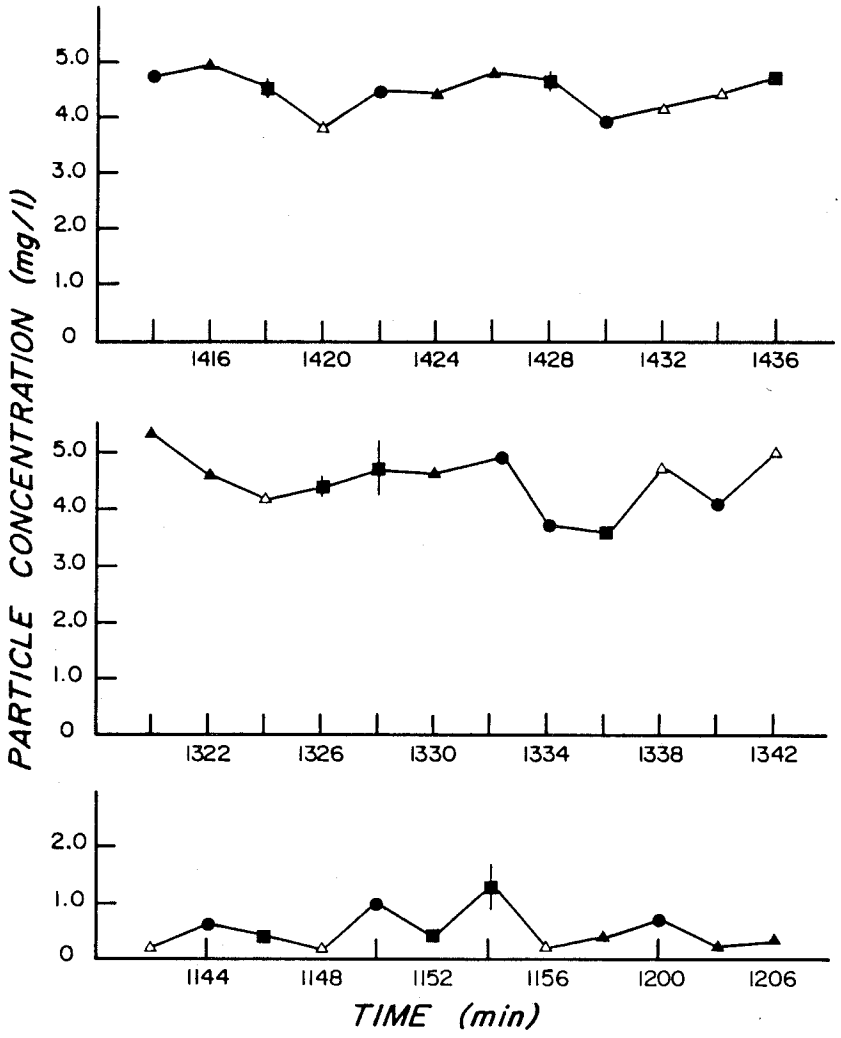


Figure 3.6: Comparison of four methods used to sample the water column for particles during three time intervals of the 5/26/82 series. One comparison (C) was made before the flow had been seeded with beads; the other two comparisons (A and B) were made, during different time intervals, while the flow was continuously seeded with 46-μm beads. Three samples by each of the four methods (described in the text) were taken, one every 2-min, in random order over each 24-min interval. For the paired samples collected by the peristaltic pump, vertical bars connect the range in values for each pair. The mean values for the pump samples are connected, by horizontal lines, to the single water samples collected by the other sampling methods. On this figure the solid squares are for peristaltic pump samples, the solid circles for samples taken with tenite butyrate cylinders, the solid triangles for 300-ml bottle samples and the open triangles for 500-ml bottle samples.

over each 24-min interval. These observations were tested statistically for the three methods, (peristaltic pump samples, tenite butyrate cylinders, and 300-ml bottles) that collected similar sample volumes (250 to 350 ml). The three particle concentrations from a single sampling method are treated as replicate estimates of the mean particle concentration over each 24-min interval. The two samples collected simultaneously at a given 2-min interval by the paired tubes of the peristaltic pump sampler are averaged, giving a single estimate of the particle concentration, at that point in time, that is comparable with the single time-point estimates taken by the other sampling methods.

The null hypothesis (H_0) that there is no difference between the mean particle concentrations estimated by the three sampling devices over each 24-min interval was tested using the nonparametric Kruskal-Wallis one-way analysis of variance (see Section 3.2.8). In all cases the H_0 could not be rejected at $\alpha \leq 0.05$. Thus, no statistically significant differences between particle concentrations estimated by the three sampling methods (that collected similar sample volumes) were detected, suggesting that biased sampling by these methods is unlikely.

Of the hand-held samplers, the tenite butyrate cylinders took a water sample most quickly (filling in ~ 2 sec), with the 300-ml bottles taking slightly longer to fill. The peristaltic pump was the slowest sampling method; 9-10 sec were required at maximum pumping speed (28.8 cm/sec) to take approximately a 250-ml sample. However, several other aspects to the pump sampler made it the preferred

sampling method: (1) The pump sampling tubes present the smallest cross-sectional area to the flow and, thus, cause the least amount of flow obstruction at the height of the trap mouth. (2) The frame holding the sampling tubes was clamped onto a vertically traversing vernier scale facilitating accurate positioning of the tubes at the same height above the bed each time the apparatus was lowered into the water. (3) The pump sampling tubes were not hand-held, but were mechanically lowered into the flume, eliminating possible contamination of the water or flow disturbances associated with immersing a sampling jar into the water by hand. (4) A pair of samples is taken at each time interval yielding replicate estimates of particle concentration in the water mass. (5) Samples are quickly pumped into small (~ 250-ml) collecting jars so that many samples can be taken, closely spaced in time.

Water samples were pumped from the flume at mean sampling speeds of 28.8 cm/sec, with a standard deviation (SD) of 1.2 cm/sec, for N = 12 measurements (hereafter, the calculated SD will be indicated by a "±" following the calculated mean). The sampling speeds of each of the paired tubes were determined by measuring the volume of water collected in 2.3 to 2.9 sec. The two tubes sampled at similar speeds; in six replicate measurements one tube sampled at 29.1 ± 1.3 cm/sec and the other tube at 28.2 ± 0.5 cm/sec. These speeds were achieved at the maximum setting on the peristaltic pump.

The maximum pumping rate was chosen to minimize the sampling interval and, thus, the duration of upstream disturbances to the flow field. Because this water sampling speed was nearly three times the

flume flow speed, possible oversampling of particles at these high sampling speeds was tested by taking water samples at slower pumping rates.

During five 8-min intervals for two series, paired water samples were collected 2-min apart at four different peristaltic pump sampling speeds, ranging from 6.5 to 28.8 cm/sec (Figure 3.7). During each interval, the H_0 that there is no difference between particle concentrations in water samples taken at the four pumping speeds was tested against the ordered alternative hypothesis (H_a) that particle concentration in water samples increases with increasing pump sampling speed. In all five speed comparisons, the H_0 could not be rejected, even at $\alpha \leq 0.10$, using the nonparametric Jonckheere test (see Section 3.2.8). In fact, the lowest α-level at which the H_0 could be rejected was $\alpha \leq 0.19$ (for the data points plotted in the top line on Figure 3.7).

The empirical conclusion that a pump sampling speed approximately three times the flume flow speed does not result in over collection of particles is also supported theoretically (see Appendix I). The particles used to seed the flume flow closely follow the flow streamlines, accelerating nearly instantaneously when the flow accelerates (as when a water sample is taken). The particles do not have enough inertia to allow significant overcollection of particles when higher-than-ambient flow speeds are used to pump water samples from the flume.

The volume of water collected in peristaltic pump samples during trapping experiments usually varied between 200 and 250 ml. During

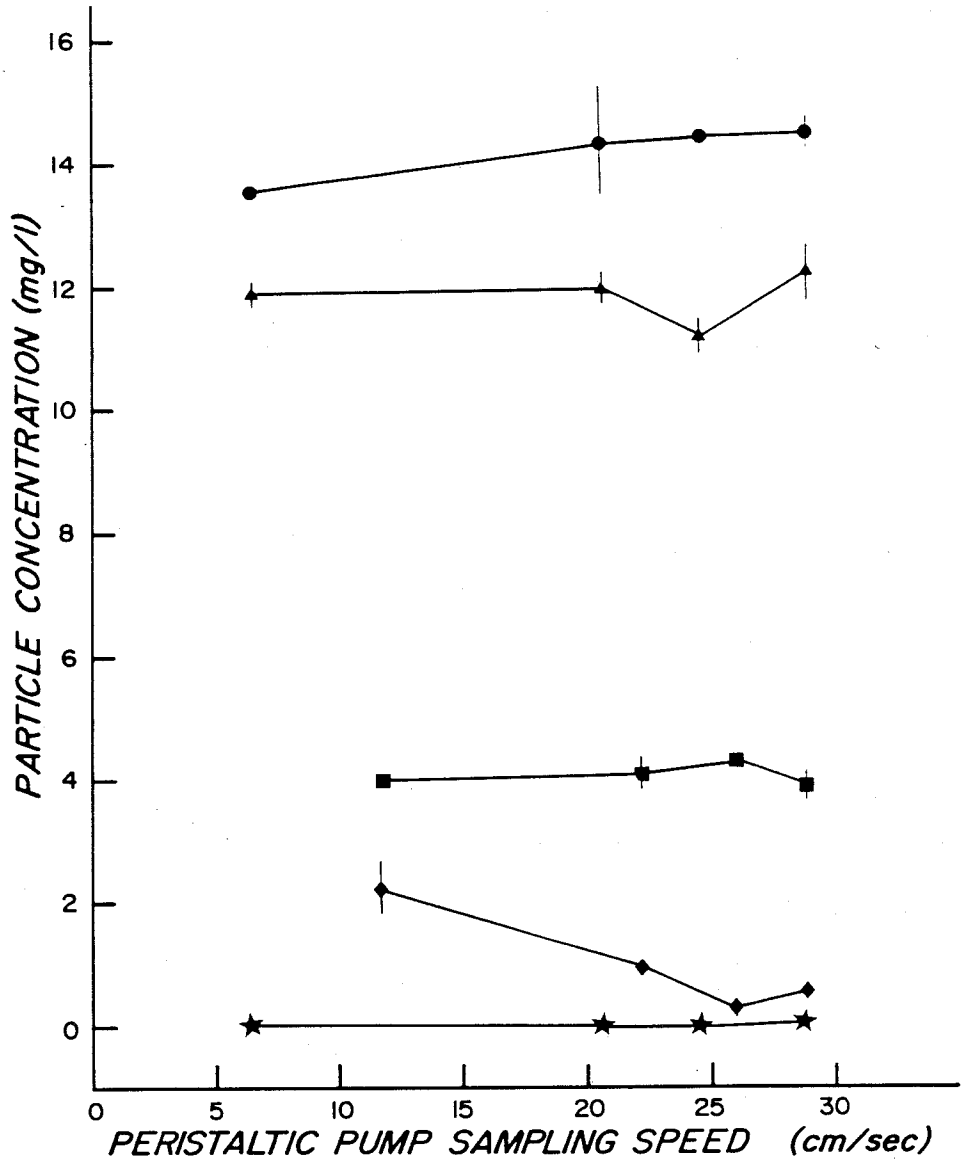


Figure 3.7: Effect of pump sampling speed on particle concentration in water samples collected over five 8-min intervals during the 5/26/82 and 6/24/82 series. For each comparison, samples were taken 2-min apart, the order of the sampling speeds randomized over each 8-min interval. The range of values for each pair of samples collected at the 2-min intervals are connected by vertical bars; horizontal lines connect the mean values. Samples were taken before beads were added to the flume during both the 5/26/82 series (diamonds) and the 6/24/82 series (stars). Samples were taken during one time interval while the flow was continuously seeded with 46-μm beads during the 5/26/82 series (squares) and during two time intervals while the flow was continuously seeded with 25-μm beads during the 6/24/82 series (circles and triangles).

sampling, the pumping apparatus (the paired sampling tubes mounted on a frame, see Figure 3.4) was in the flume for $\leq$ 30 sec, the time partitioned approximately as follows: 5 sec to lower the frame into the water, 10 sec to purge the tubing of water from the previous sampling (i.e., water was pumped into a dish and discarded), 9 sec to take a sample, and 5 sec to raise the frame out of the water.

The water was pumped into glass jars that were prewashed and rinsed twice with prefiltered (using 0.45-μm Metricel filters) deionized water. These samples were stored in a cold box at 6 ± 1 °C until filtering (within 10 days of the experiment). The samples were first measured for water volume to ± 1 ml, and then filtered through preweighed 0.45-μm Millipore filters using a vacuum pump. The filters were air-dried and weighed to ± 0.001 mg and rounded to .01 mg due to the precision of the scale. The weights also were corrected for changes in humidity (see below).

Short water sampling times were required to minimize disturbances to the upstream water mass during trap collections and small sample volumes were required to minimize sample-processing time (filtering water samples). However, samples large enough to minimize analytical error were also necessary. For example, the error in particle concentration estimates decreases as sample volume and the weight of beads on a single filter increases; but too many beads on a filter results in increased analytical error because a portion of the beads roll off the filter during the weighing procedure.

A careful analysis of the errors associated with all aspects of the sample processing (e.g., the precision of the scale, the

efficiency of the filtering process, and the characteristics of the filters before and after filtering) revealed that the largest source of error is the humidity correction term. This correction factor is applied to the filter weights to account for changes in humidity that occurred between the first and the second weighings. This error was estimated to be approximately ± 0.14 mg (the origin of this number is discussed in detail in the following two paragraphs). The impact of this error term on measurement precision clearly depends on the weight of beads on a filter. To maintain this error below 10 percent, a sample containing a minimum of 1.50 mg of beads is required. Thus, water samples of at least 190 ml had to be collected because the trapping experiments were designed for flume particle concentrations ranging from 8 to 12 mg/l.

The common procedure of pairing all filters so that the top filter collects particles and the bottom filter serves as an uncontaminated "reference" for weight changes in the filter due to changes in humidity alone, was not used in the present study. A study of humidity changes in paired "control" (filtered with 100-ml of 0.22-μm prefiltered water) filters showed that while both filters would either lose or gain weight, the absolute weight changes in the top and bottom filters of a given pair were always different. For the five pairs of filters tested, the difference in weight change between top and bottom filters was 0.01 to 0.09 mg; between the five bottom filters this difference was 0.02 to 0.11 mg and between the five top filters it was 0.01 to 0.08 mg. It appears that there is no increase in precision conferred by pairing filters and applying a

correction factor to the top filter based on the weight change of the bottom filter, relative to the precision associated with applying a correction factor for the weight change of any other reference filter. In fact, statistically, the mean weight change for a group of reference filters has a higher probability of representing the "true" weight change of any top filter experiencing the same humidity conditions.

In the present study, for a "lot" (approximately 100 filters packaged in the same box by Millipore and having the same factory lot number) of filters, the first filter removed from the box and every tenth filter after that was paired with a reference filter (usually there were 10 reference filters per lot). To insure that the range in humidity changes on the reference filters represents the range in humidity conditions experienced by the 100 filters, the filters in a lot were always weighed sequentially over a 2-hr period both before and after drying. The mean humidity change for the 10 reference filters was used as the humidity correction factor for each filter in the lot. The mean error of 0.14 mg ± 0.06 mg associated with this humidity correction procedure was calculated from the standard deviation of the mean humidity changes for the 26 lots of filters used in trapping experiments throughout the study.

The purpose of taking discrete samples from the upstream water mass at the height of the trap mouth, over time, is to determine an average concentration of particles available for trap collections. Thus, the patchiness of particles in the water approaching a trap is another important consideration for water sampling design.

Maintaining a well-mixed water mass upstream of the test section may adequately homogenize bead concentrations in the flume, but does not necessarily eliminate particle patchiness. Although the flume was drained and cleaned between each series, dust particles and rust from the pipes invariably appeared. In addition, the flume was filled with water from the Cambridge City system that was filtered only through a diotomaceous earth filter. Efforts to pump this ~ 10,000-liter water mass through garden hoses connected to 3-μm swimming pool filters for a 19-hr period did not substantially reduce "background" (prior to bead additions) particle concentrations. Thus, although background concentrations were usually between 0.5 and 1.5 mg/l (see column 3 in Table 3.10), occassional concentrations of $\geq$ 1.5 mg/l were detected. Water samples must be either large enough or frequent enough to adequately represent this variability in particle concentration.

To determine the effect of sample volume (and, thus, also of sampling duration) on estimates of particle concentration, during two 8-min intervals water samples of four different volumes ranging from ~ 145 to ~ 880 ml were collected (see caption to Figure 3.8). During both intervals the 145-, 290-, and 410-ml samples collected similar concentrations of material (Figure 3.8). However, the 880-ml samples collected ~ 1 mg/l more material than the other three sample volumes both before and after the flow was seeded with beads. This suggests that sampling the water for a longer period of time increases the probability of collecting one of the relatively large patches of background particulates that are periodically present in the flow. The error that may be introduced by taking smaller samples depends on

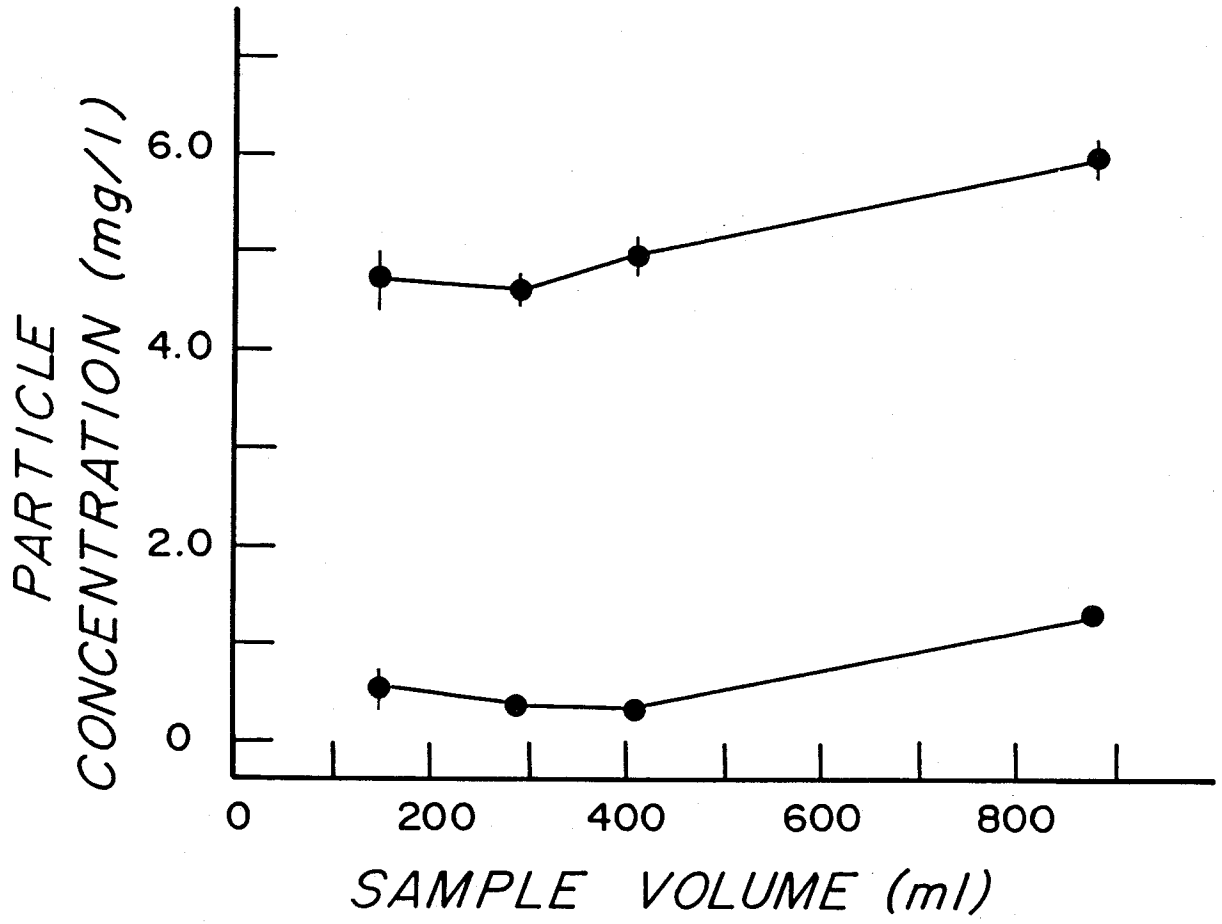


Figure 3.8: Effect of pump sampling volume on particle concentration in water samples collected over two 8-min intervals during the 5/26/82 series. All samples were pumped at the same speed (28.8 cm/s), but for different periods of time: 5 sec (~ 145 ml), 10 sec (~ 290 ml), 15 sec (~ 410 ml) and 30 sec (~ 880 ml). Samples were taken 2-min apart, the order of the volumes randomized over each 8-min interval. The range of values for each pair of samples collected at the 2-min intervals are connected by vertical bars; horizontal lines connect the mean values. Samples were taken before beads were added (lower line) and while the flow was continuously seeded with 46-μm beads (upper line).

the concentration of particles in the flow. In water samples taken before beads were added to the flume, the 880-ml samples collected 222 percent more material than in the average collections by the three smaller-volume samples. In the water samples taken while the flow was continuously seeded with 46-μm beads at concentrations of 4-5 mg/l, the 880-ml samples collected only 26 percent more material than the smaller-volume samples. Because the particle concentrations during trapping experiments usually ranged from 8 to 12 mg/l, the ~ 1 mg/l spike of particulates periodically missed in small sample volumes would represent an error of only 8 to 12 percent.

Sample volumes of 880-ml taken every 2-min were prohibitive in the present study because of the required duration of sampling (the upstream flow would be disturbed ~ 30 percent of the time), the sample processing time, and financial constraints. However, the volume comparison study actually indicates the proportion of the time, during an 8-min interval, that the water passing through the sampling space must be collected to most accurately reflect the true mean concentration during that interval. Sampling 6.25 percent of the time (30 sec of sampling during an 8-min interval) was long enough so that periodic spikes in particle concentration were represented in mean concentration estimates; sampling from 1.04 to 3.12 percent of the time was not long enough to include these spikes. To match the sampling characteristics of the 880-ml samples using shorter sampling intervals (and volumes), the sampling frequency must be increased. Thus, in the present study, background particle concentrations during flume experiments were estimated using

~ 9-sec samples (volumes of 200-250 ml) taken every 111 sec (i.e., at ~ 2-min intervals) so that 7.5 percent of the water passing through the sampling space was collected.

Prior to seeding the flow with beads in each series, the flume flow was sampled every 2-min for a 22-min interval. These 11 pairs of concentration estimates were used to determine the mean background concentration for the series. A separate background concentration was determined for each series to allow for possible differences between series in Cambridge City water quality and flume cleanliness.

Estimates of the mean background concentration were not substantially improved if the water was sampled for a continuous interval > 22 min. In the 8/24/82 series, water samples were taken every 2 min for 22 min and then every 4 min for the next 40 min. The mean (± SD) background concentrations for the 22-min and the entire 62-min interval were essentially identical: 1.44 (± 0.33) mg/l for N = 22 observations and 1.37 (± 0.34) mg/l for N = 42 observations. However, a water-sampling interval < 22 min was not long enough to adequately represent the variability in background particle concentrations. Over an 8-hr period during the 5/25/-5/26/82 series, the water was sampled every 2-min for a 10-min interval every other hour (totaling five sets of samples). The mean (± SD) background particle concentration for the N = 10 samples in each set was 1.13 (± 0.41) mg/l, 0.58 (± 0.40) mg/l, 0.73 (±0.11) mg/l, 0.82 (± 0.30) mg/l, and 0.74 (± 0.20) mg/l. The H_0 that these means were all drawn from the same population was rejected at $\leq$ = 0.05 using the nonparametric Kruskal-Wallis test (see Section 3.2.8).

3.2.6 Trap tests

The relevant dimensions of the traps tested in the flume are given in Table 3.1; hereafter the traps will be referred to by the code numbers listed in this table. The "tenite butyrate" traps were cut from lengths of clear tenite butyrate tubing. The bottoms were cut from clear acrylic plastic (8-mm thick) for traps TBC14.7-2.9, TBC14.7-1.6, and TBF14.7-1.6. For traps TBC1.7-3.0, TBC3.6-3.1 and TBC7.4-2.9, polyethylene plastic caps for the tubing were used to seal the trap bottoms. The "opaque plastic" traps were screw-cap polyethylene jars with threaded trap mouths (the tenite butyrate traps were straight-sided at the trap mouth). Several trap designs were made by gluing (using silicone sealant or waterproof epoxy) two jars together: trap OPC8.5-2.7 consisted of trap OPC8.5-1.0 glued on top of trap OPC8.5-1.9, trap OPC8.5-3.6 was made from two trap OPC8.5-1.9 glued together, a funnel was glued inside trap OPC8.5-1.0 and then taped on top of another trap OPC8.5-1.0 to make trap OPF8.3-1.9, and trap OPC8.5-1.0 was glued on top of trap OPG8.3-3.0 to make trap OPGC8.5-3.6. Jars were affixed together by cutting the bottom off the upper jar and sliding this straight-sided cylinder over the threaded mouth of the lower jar; the glue was applied between the two jars and inside the trap so that a ridge (~ 1-mm wide) protruded ~ 2-mm above the inside perimeter of the trap. Jars were affixed in this way so the traps would still present a smooth surface to the oncoming flow.

The specific trap designs tested in a given series are listed in the second column of Table 3.10. In each case, three replicates of

each trap design were tested. During series 7/10/82, 7/22/82 and 8/24/82, the order of testing replicates of all trap designs was determined from a random-number table. For series 6/24/82, replicates of the two trap designs (see Table 3.10), tested for each of the 4.5-, 6.5-, 8.5-, and 16.5-min intervals, were randomized over the whole series. However, during series 6/7/82, all traps collecting for 4.5-min intervals were tested successively, followed by all traps collecting for 6.5-min intervals, and then for 8.5-min intervals; replicates of the four trap designs (see Table 3.10) were randomized, separately, within these three blocks of time.

Before testing, all traps were first scrubbed with a bottle brush, then rinsed several times with prefiltered (through 0.45-μm Metricel filters) deionized water and capped. A trap was lowered into the water, secured in the basket on the pedastal and then the cap was removed to mark the start of the "collecting interval." At the end of the collecting interval the trap was capped in place and then removed from the flume. Traps were stored in a cold room at 6 ± 1°C and processed as for the water samples (see Section 3.2.5).

Traps collected beads for intervals of ~ 8.5 min; this collecting interval was experimentally determined as the minimum period of time necessary for trap collections to reach steady state (Section 3.3.4). Three pairs of water samples were taken during each trap collecting interval: one pair immediately after the trap was uncapped in the flume, one pair at the midpoint of the interval, and one pair immediately before capping the trap at the end of the interval. Thus, the three pairs of bead concentration estimates were

taken ~ 4-min apart. The water mass upstream of a trap was disturbed during ~ 17.6 percent of each collecting interval (three ~ 30-sec disturbances in 8.5 min) due to water sampling. Care was taken to slowly and smoothly lower and raise the pump sampling apparatus during trap collections to minimize these disturbances. Usually 2 min lapsed between adjacent trap collections.

Measuring bead concentrations in the flume at the beginning, midpoint, and end of each collecting interval (yielding a total of N = 6 water samples from the paired sampling tubes for each trap collection) characterizes the variability in bead concentrations over the entire interval and also minimizes disturbances to the upstream water mass. To determine if an increased sampling frequency would substantially improve estimates of mean bead concentrations during the collecting intervals, for the 6/7/82 and 6/24/82 series water samples were taken every 2 min during all collecting intervals. For the 8.5-min collecting intervals estimates of mean bead concentrations from five pairs of water samples (N = 10 estimates of bead concentration) were compared to estimates of the mean from the three pairs (N = 6) of samples taken at the beginning, midpoint and end of the intervals.

Increasing the sampling frequency resulted in very small changes in both the mean and the standard deviation of bead concentrations (Table 3.2). For the 6/24/82 series, the changes in mean bead concentration for N = 6 samples were only 0.1 to 2.0 percent of the mean for N = 10 samples; the net changes in the percent CV of the mean were also very low, between 0.2 and 1.9. For the 6/7/82 series,

TABLE 3.2

Effect of Sampling Frequency on Estimating Mean Bead Concentrations During 8.5-min Trap Collecting Intervals of the 6/7/82 and 6/24/82 Series[1]

Collecting interval[2]		Mean bead concentration (mg/l)	SD (mg/l)	N[3]	Percent CV	Percent change in mean[4]	Net change in percent CV[5]
Series 6/7/82							
OPC8.5-1.0	1	4.97	1.09	9	21.9	6.2	- 1.1
		5.28	1.10	6	20.8		
	2	5.39	0.36	10	6.7	0.7	+ 0.9
		5.43	0.41	6	7.6		
	3	5.14	0.49	10	9.5	3.5	+ 2.4
		4.96	0.56	6	11.9		
OPC8.5-1.9	1	6.09	0.32	8	5.2	2.3	- 1.0
		6.23	0.26	5	4.2		
	2	6.16	0.90	8	14.6	0.6	+ 7.0
		6.12	1.32	4	21.6		
	3	4.78	0.41	10	8.6	1.5	- 2.4
		4.85	0.30	6	6.2		
OPC8.5-2.7	1	5.41	0.51	10	9.4	0.2	+ 3.0
		5.42	0.67	6	12.4		
	2	5.54	0.62	10	11.2	2.0	+ 1.2
		5.65	0.70	6	12.4		
	3	4.88	0.25	9	5.1	1.0	- 1.6
		4.83	0.17	6	3.5		
OPF8.5-1.9	1	6.23	0.25	9	4.0	0.3	+ 0.8
		6.25	0.30	6	4.8		
	2	4.92	0.53	10	10.8	1.0	+ 2.3
		4.87	0.64	6	13.1		
	3	5.55	0.72	10	13.0	1.3	+ 2.1
		5.62	0.85	6	15.1		

TABLE 3.2 (cont. - 2)

Collecting interval[2]		Mean bead concentration (mg/l)	SD (mg/l)	N[3]	Percent CV	Percent change in mean[4]	Net change in percent CV[5]
Series 6/24/82							
OPC8.5-2.7	1	11.39	0.79	10	6.9	1.6	+ 1.7
		11.21	0.97	6	8.6		
	2	10.36	0.44	10	4.2	0.6	- 1.2
		10.30	0.31	6	3.0		
	3	11.20	0.44	10	3.9	0.2	+ 0.6
		11.18	0.50	6	4.5		
	4	10.82	0.65	10	6.0	2.0	- 0.4
		11.04	0.62	6	5.6		
	5	14.61	0.64	10	4.4	0.1	- 0.2
		14.59	0.61	6	4.2		
	6	15.18	0.61	10	4.0	0.2	+ 0.4
		15.15	0.67	6	4.4		
OPC8.5-3.6	1	13.45	0.59	10	4.4	0.4	+ 0.9
		13.50	0.71	6	5.3		
	2	14.06	0.78	10	5.5	0.4	+ 1.9
		14.12	1.04	6	7.4		
	3	11.25	0.93	10	8.3	1.2	+ 1.2
		11.39	1.08	6	9.5		

1. 46-μm beads and 25-μm beads were used to seed the flows in the 6/7/82 and 6/24/82 series, respectively.
2. Arranged here by replicate of the trap design tested during the interval.
3. During each 8.5-min interval, five pairs of water samples were collected, one pair every 2-min yielding a total of N = 10 bead concentration estimates. Listed in this table are the mean and SD for all N = 10 estimates and for just the pairs of samples taken at the beginning, midpoint and end of each interval (N = 6 estimates). Occassionally one (in two cases, two) estimate was discarded because of sampling or processing errors.
4. The percent change relative to the largest number of samples taken (usually N = 10).
5. Calculated as CV for N = 10 minus the CV for N = 6.

the variability in bead concentrations was greater due, in part, to the lower concentration of beads in the flume compared to other series (e.g., see last column of Table 3.10). Still, an increased sampling frequency only slightly improved mean bead concentration estimates in the 6/7/82 series. The changes in mean bead concentrations for N = 6 samples were only 0.2 to 6.2 percent of the mean for N = 10 samples; the net changes in the CV were 0.8 to 7.0 percent. Thus, pairs of pump samples taken at the beginning, midpoint and end of each collecting interval adequately described the variability in bead concentration over the interval.

3.2.7 Calculations of relative particle collection efficiencies

The particle collection efficiencies (E) of the various trap designs tested in the flume were calculated by dividing the corrected weight of beads collected in a trap (B_t) by a predicted collection estimate (B_p). The relative particle collection efficiencies (E_r) were obtained by normalizing the particle collection efficiencies for all trap designs tested in a given series by the mean particle collection efficiency (E_s) for trap OPC8.5-2.7 in that series. This was necessary because differences in conditions between the series resulted in different mean particle collection efficiencies for trap OPC8.5-2.7, the only trap design tested in all series (see Section 3.4.4). In order to compare collection efficiency estimates of traps tested in different series, the efficiency estimates were standardized by the mean collection efficiency of this trap design.

B_t, the weight of beads collected by a trap, is the final

measured weight of beads in a given trap (B_f, the beads collected on the 0.45-μm filters) minus a correction term, B_w. B_w is the weight of beads contained in the water sample collected when a trap was initially uncapped at depth. To estimate B_w, the measured volume (ml) of water (V_t) in a trap was multiplied by the mean concentration (mg/l) of all particles in the water during the trap collecting interval (C_{ap}). The correction term, B_w, was necessary because of the short trap collecting intervals in the flume relative to the field (see next paragraph).

Traps are used to measure the time-integrated vertical flux of particles through a particular sampling space in the water column. For calculations of B_p, the trap mouth is treated as a flat surface; particles must fall through this surface to be considered part of the vertical flux. When a trap is first uncapped at depth, water rushes in to fill the air space. Particles in this initial water sample did not "fall" through the trap collecting surface. In fact, some of these particles may have fallen below the trap mouth and entered the trap in the initial water sample by suction alone. Technically, these particles constitute part of the vertical flux from a time point prior to when the trap was uncapped in the water. Thus, for measures only of the vertical flux collected by a trap, from the time it is uncapped to the time it is sealed, particles in the initial water sample must be excluded.

In the field the proportion of particles collected by a trap in the initial water sample is very small compared to the vertical flux of particles during the collecting interval. For example, in field

environments with a constant particle concentration of 10 mg/l, an 8.5-cm diameter trap accurately collecting particles (that is, acting as an unbiased collector) over a 24-hr interval, would contain a vertical flux of 2451.38 mg (assuming the particles had fall velocities of 0.05 cm/sec and using eq. 3.1, given below, for calculating B_p). If the trap volume is 1000 ml, then the weight of beads contained in the water sample initially taken by this trap would be 10 mg. Thus, the proportion of beads collected in the initial water sample relative to the beads contained in the vertical flux would be 0.4 percent. However, this same trap collecting for an 8.5-min interval under identical conditions in the flume would contain 15.32 mg in vertical flux; the initial water sample would then be 65.3 percent of the total beads collected in the trap.

B_p was calculated as

$$(W_c)\ (T_i)\ (A_t)\ (C_i) \tag{3.1}$$

where W_c = the calculated fall velocity (cm/sec) of the mean bead diameter in the bead mixture used to seed the flow, T_i = the length (sec) of the trap collecting interval, A_t = the inside trap mouth area (cm^2), and C_i = the mean bead concentration ($mg/10^3cm^3$) during the trap collecting interval. $C_i = C_{ap}-C_{bp}$, where C_{bp} is the mean background particle concentration for the series. All of these quantities, except particle fall velocity (W_c), were measured in the study. The error terms associated with each of these measurements are presented in Section 3.4.3.

W_c was not measured, but was calculated from Stokes'(1851)

equation,

$$d = \frac{0.75\ C_D\ W_c^{\ 2}\ \rho_f}{(\rho_p - \rho_f)\ g}\ , \tag{3.2}$$

$$C_D = \frac{24}{R_p}\ , \tag{3.3}$$

$$R_p = \frac{d\ W_c\ \mu_f}{\rho_f}\ , \tag{3.4}$$

where d = particle diameter, ρ_f = water density, ρ_p = particle density, g = acceleration due to gravity, C_D = particle drag coefficient, R_p = particle Reynolds number, and μ_f = water viscosity. Stokes equation is considered valid for spherical particles with $R_p < 1$ falling through Newtonian fluids. All beads used in this study meet these criteria.

In calculations of W_c for each series of trapping experiments, d = the mean bead diameter (as determined in Figure 3.5) for the bead mixture used in the series. In calculations of B_p, the repercussions of using a particle fall velocity based on the mean bead diameter, when particles with fall velocities covering one or two orders of magnitude (see Figure 3.9) were used to seed the flows, is discussed later (Section 3.4.3).

The other variables that must be estimated to calculate W_c are μ_f and ρ_f. By substituting (3.3) and (3.4) into (3.2) and rearranging the terms, the relationship between W_c, μ_f, and ρ_f is more obvious,

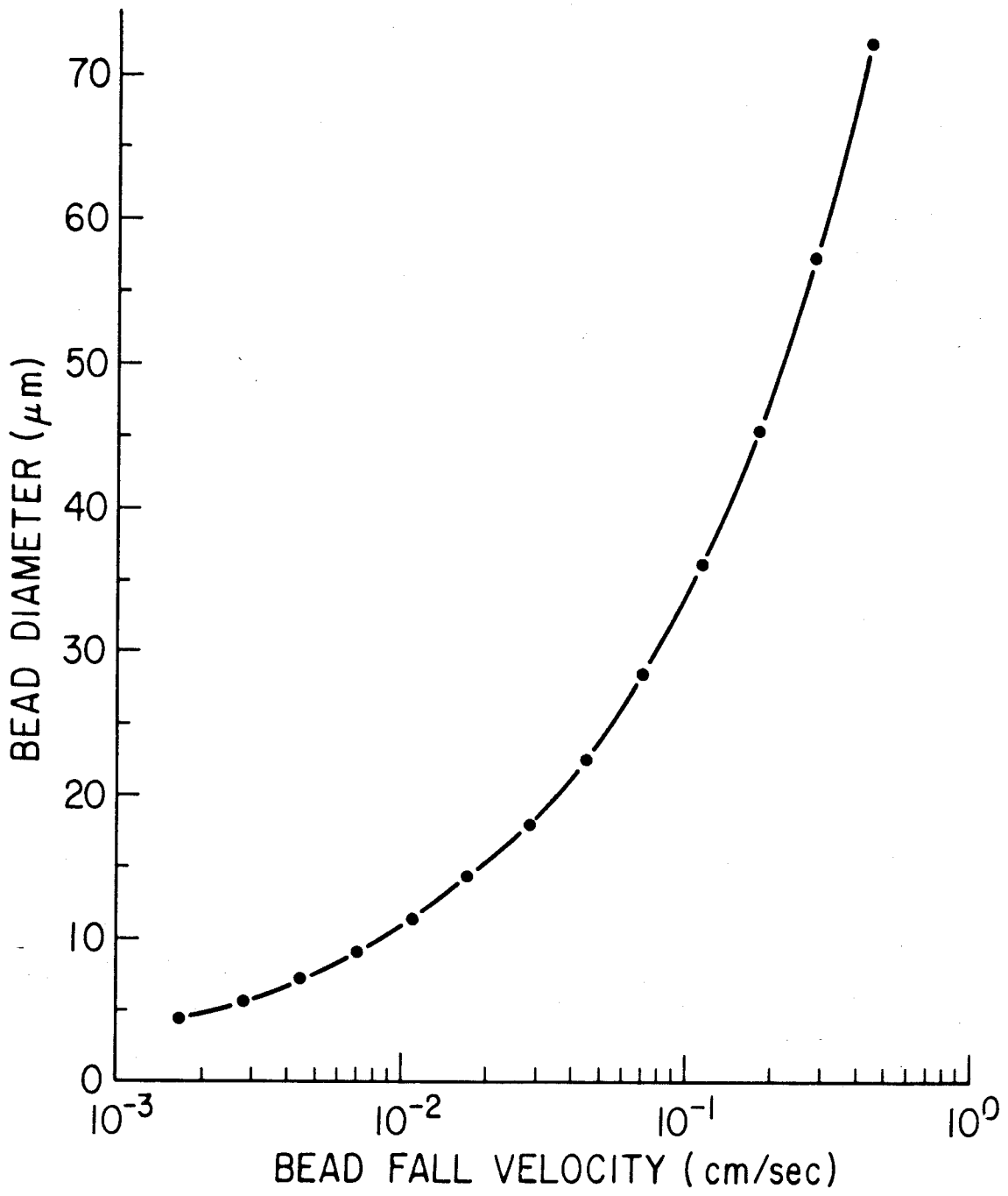


Figure 3.9: Calculated fall velocities for bead diameters at the midpoint of each Coulter-Counter size class in the 25-μm and 46-μm bead mixtures (see Figure 3.5 for size-frequency histograms of the bead mixtures). Fall velocities were calculated from Stokes equation for freshwater at 24°C and atmospheric pressure, $\mu_f = 0.911 \times 10^{-2}$ g/(cm)(sec), $\rho_f = 0.9973$ g/cm^3, $\rho_p = 2.42$ g/cm^3, and $g = 9.807 \times 10^2$ cm^2/sec.

$$W_c = \frac{d^2 (\rho_p - \rho_f) g}{(0.75) (24) (\mu_f)} . \qquad (3.5)$$

Water temperature in the flume varied from 20 to 28°C between all series of trapping experiments and usually warmed ~ 2°C during a series (see Table 3.10). ρ_f decreases from 0.998203 g/cm^3 to 0.995944 g/cm^3 over this temperature range, or by ~ 0.2 percent. This small change in ρ_f has a negligible effect on the value of W_c, especially because ρ_p (2.42 g/cm^3) is large compared to ρ_f anyway. However, μ_f decreases from 1.002×10^{-2} g/(cm)(sec) at 20°C to 0.8327×10^{-2} g/(cm)(sec) at 28°C or by ~ 20 percent. Because μ_f and W are inversely related (see eq. 3.5), a 20 percent decrease in μ_f will result in a 20 percent increase in W_c.

The calculated values for W_c are plotted versus water temperature for bead diameters of 24.85 and 46.41 μm in Figure 3.10. For a given trap collection, the W_c used in calculating B_p was taken from this figure for the water temperature at the midpoint of the trap collecting interval. Water temperature was measured only about every hour during each series; however, the water warmed at a relatively constant rate (0.3 to 0.5°C per hour, see Table 3.10) each day. Thus, the water temperature (± 0.1°C) at the midpoint of each trap collecting interval could be calculated.

3.2.8 Statistical tests used in this study

Only nonparametric statistical tests were used in this study so no underlying distributions (e.g., the normal distribution) in the data were assumed. Nonparametric tests were chosen because the sample sizes were small for most of the measurements (e.g., three

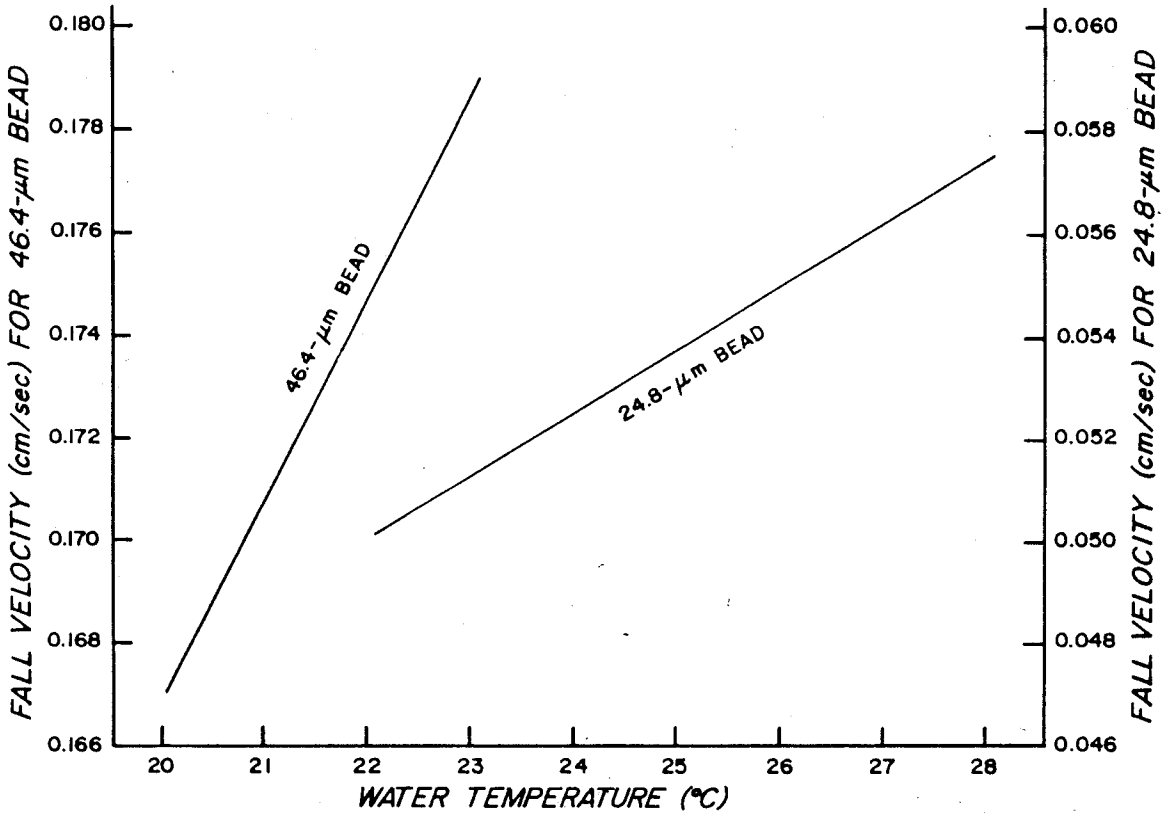


Figure 3.10: Relationship between particle fall velocity and water temperature for the mean bead diameters (46.4 and 24.8 μm) in the two bead mixtures and for the range of water temperatures that occurred during flume experiments (see Table 3.10). Fall velocities were calculated from Stokes equation for freshwater at atmospheric pressure, ρ_p = 2.42 g/cm^3, and g = 9.807x10^2 cm^2/sec. Values for μ_f and ρ_f at the water temperatures plotted here were taken from the Handbook of Chemistry and Physics (51st edition).

replicate estimates of E_r for each trap design tested during a series) and the underlying distributions for many of the measured values (e.g., particle concentration) or calculated values (e.g., trap Reynolds number) were unknown. Nonparametric tests are conservative, that is, they are less likely to commit an α-error (reject a true H_0) compared to parametric tests; thus, nonparametric tests are also less powerful (i.e., they are more likely to commit a β-error and accept a false H_0) than parametric tests.

The statistical tests used in this study are listed below. For all of these tests the data are ranked and probabilities are calculated that the observed differences between the ranked data would occur, by chance alone, if the data are all drawn from the same population. All of these tests are described in a standard nonparametric statistics text, such as Siegel (1956), except where noted.

For tests between two classifications of the data (i.e., between two means), the Mann Whitney U-test is used. The Kruskal-Wallis one-way analysis of variance is used for tests between several classifications (several means) when no a priori H_a can be selected. However, when an ordered a priori H_a can be stipulated, the Jonckheere (or Terpstra) test (described in Hollander and Wolfe 1973) is the more powerful nonparametric test for differences between more than two means. To test for a particular trend in individual data points, Mosteller's test of predicted order (described in Sarris and Wilkening 1977) is used. For this test, an a priori predicted order is chosen and then the binomial probability is calculated that

this particular order will occur the observed number of times, by chance alone. (Sarris and Wilkening [1977] provided several extensions of Mosteller's approach and Hsu [1979] corrected some of the calculations made by Sarris and Wilkening.) For correlations between two data sets, the Spearman rank correlation coefficient (r_s) is calculated.

In general, statistical differences between data are tested at the 95 percent confidence level ($\alpha \leq 0.05$). However, in many cases, the exact α-levels for which the H_0 can or cannot be rejected are given, for the following two reasons. (1) Because differences between the exact values of the data are not tested using nonparametric statistics (e.g., the data are converted to ranks for all the tests mentioned above), α-levels are limited to the discrete probabilities that ordinal differences will occur. In parametric statistics, probabilities are calculated for a continuous normal distribution. For example, using the Mann Whitney U-test for $N = 3$ estimates of two classifications of the data, discrete probabilities can be calculated that overlap will occur between one, two, or three of the data points in each classification; using parametric statistics, a continuous probability spectrum is available in the t-test. Critical values of the t-statistic always can be determined for $\alpha \leq 0.05$ but critical values of nonparametric statistics are almost never associated with the exact probability of, for example, $\alpha \leq 0.05$. Thus, the discrete probabilities associated with critical values of the nonparametric statistics are usually given in this study. (2) Using $\alpha \leq 0.05$ as the highest acceptable level for

rejecting the H_0 is a somewhat arbitrary figure. For data that can be measured with $\leq$ 5 percent error and that are not inherently more variable than ± 5 percent, perhaps a confidence level of 95 percent for detecting differences between means is reasonable. However, at least 10 percent error is associated with many of the values that were either measured or calculated in the present study (see Sections 3.4.1 and 3.4.3); detecting differences at $\alpha \leq 0.10$ then may be the lowest reasonable α-level to expect of these data. Likewise, if data can be measured with 99.9 percent precision and accuracy, then rejecting the H_0 at $\alpha \leq 0.001$ would probably be the most conservative procedure. However, in many cases it is not possible to determine the most reasonable α-level for rejecting the H_0, so the exact probabilities associated with the critical values of the nonparametric statistics used in this study usually are given.

To determine the precision of a given measurement, coefficients of variation (CV) are calculated as percentages of the mean (percent CV is 100 times the standard deviation divided by the mean), whenever possible. However, when only two data points are available, or when only the end-points in a range are used, the "percent error" is estimated as one-half the range in values divided by the mean of the two values. This calculated error is a more conservative estimate, but is comparable to the CV. The percent error and the percent CV are distinguished here from the "percent difference" between two data points. The percent difference is calculated as the absolute difference between the two data points divided by one of the data points and is used when there is a priori knowledge that one or the

other of the data points is more accurate.

3.3 Results

3.3.1 Fall velocities of spherical or irregularly shaped inert particles

Prior to measuring the fall velocities of nonswimming larvae, the measurement precision of the two settling chambers was estimated using inert particles. This precision was quantified by calculations of the percent CV for repeated measurements of the same particle. In the large chamber, the descent of a particle was timed over two contiguous 50-cm intervals, but estimates from the second interval (in the bottom half of the chamber) were disregarded because of the aforementioned (see Section 3.2.2) problem of differential warming of the water around the stopcock. Thus, only the measurement precision for repeated 50-cm runs of a single particle ("between-runs" precision) could be estimated in the large chamber. However, because six horizontal lines were etched into the small chamber at 5-cm intervals above the bottom (see Figure 3.2), separate, but contiguous, 5-cm fall velocity estimates could be made during a particle's descent. Thus, the measurement precision within a run ("within-runs" precision) could be estimated in the small chamber, as well as between-runs precision estimates.

The between-runs measurement precision for "best-case" estimates (i.e., using spheres, see Section 3.4.1) in the large chamber was excellent (Table 3.3). Coefficients of variation were < 1.0 percent for replicate runs of spherical particles with W_m (the measured

TABLE 3.3

Between-Runs Precision in the Large Chamber: Fall Velocities and Other Physical Characteristics of Spherical Particles

Particle type[1]	ρ_p (g/cm^3)	d (μm)	Temperature range during runs (°C)	Number of replicate runs	W_m[2] mean ± SD (cm/sec)	Percent CV	W_c[3] (cm/sec)	Percent difference in W_m and W_c[4]	R_p[5]
Glass Sphere	2.42	230±2	12.7-13.5	30	2.30±0.01	0.6	2.05	10.9	4.3
Glass Sphere	2.42	182±2	12.4-13.0	14	1.61±0.01	0.6	1.97	18.3	2.3
Glass Sphere	2.42	232±2	12.3-12.7	30	2.27±0.02	0.9	2.06	10.2	4.2
Glass Sphere	2.42	130±2	12.3-12.4	3	0.785±0.057	7.3	0.876	10.4	0.81
Glass Sphere	2.42	139±1	12.8-13.0	3	0.994±0.021	0.2	0.949	4.5	1.1
Glass Sphere	2.42	124±2	12.8-13.0	1	0.826	-	0.815	1.3	0.83
Red Plastic Sphere	1.06	570±4	12.7-13.3	30	2.80±0.02	0.6	0.38	637	12.9
Red Plastic Sphere	1.06	514±4	13.4-14.1	33	2.44±0.01	0.6	0.33	639	10.3

1. Described in Section 3.3.2.
2. Timed over a vertical distance of 50 cm in the top half of the large chamber.
3. Calculated from a theoretical fall velocity curve for $R_p > 1$ (Grant, 1977) that approaches Rubey's (1933) empirical curve near the Stokes range, with values of ρ_f and μ_f for the water temperature at the midpoint of the range listed in this table and for a salinity of 31 ppt.
4. Calculated as a percentage of W_c.
5. Using d, W_m, and values for ρ_f and μ_f as defined in footnote 3.

fall velocity) from 0.826 to 2.80 cm/sec. The one particle with a larger CV (7.3 percent) was also the particle with the lowest W_m (0.785 cm/sec).

The between-runs measurement precision decreased (the percent CV increased) for irregularly shaped particles (Table 3.4). For natural sand grains falling at 2.01 - 2.13 cm/sec, CV ranged from 0.7 to 6.0 percent; for disc-shaped fecal pellets of the clam, Macoma balthica, falling at 3.78 - 4.29 cm/sec, CV ranged from 0.8 to 1.5 percent.

The low values of CV were not an artifact of large sample sizes (that is, the number of replicate runs) (e.g., see Tables 3.3 and 3.4). "Trumpet" diagrams are plots of the cumulative mean and SD for increasing sample sizes. These diagrams (Figure 3.11) are used here to visualize the effects of sample size on changes in the mean and SD of W_m for three spherical particles tested in the large chamber. The results indicate that increasing the number of runs to 14 or 30 does not improve estimates of the mean. In fact, the SD is essentially constant after the first run for two of the particles and after the third run for the other particle. In addition, the mean W_m values for all runs of a single particle are within the SD of the mean for all other runs; even the first estimate of W_m does not lie outside the SD of the other estimates.

The between-runs measurement error for spheres falling at 0.0566-0.0707 cm/sec in the small chamber was from 4.4 to 10.0 percent (Table 3.5). Trumpet diagrams (Figure 3.12) indicate that the variability (expressed as SD) in W_m becomes relatively constant after the second run for all three spheres. For two of the spheres

TABLE 3.4

Between-Runs Precision in the Large Chamber: Fall Velocities and Other Physical Characteristics of Irregularly Shaped Particles

Particle type[1]	Particle shape	Largest dimension (μm)	Temperature range during runs (°C)	Number of replicate runs	W_m [2] mean ± SD (cm/sec)	Percent CV
Natural Sand Grain	irregular	472	12.2 - 12.5	28	2.07 ± 0.07	3.5
Natural Sand Grain	irregular	376	12.3 - 12.5	2	2.01 ± 0.01	0.7
Natural Sand Grain	irregular	346	12.6 - 12.9	2	2.13 ± 0.13	6.0
Macoma balthica fecal pellet	disc	626	11.8 - 12.1	3	4.29 ± 0.04	0.8
Macoma balthica fecal pellet	disc	650	11.8 - 12.1	3	3.78 ± 0.06	1.5

1. Described in Section 3.2.2.
2. Timed over a vertical distance of 50 cm in the top half of the large chamber.

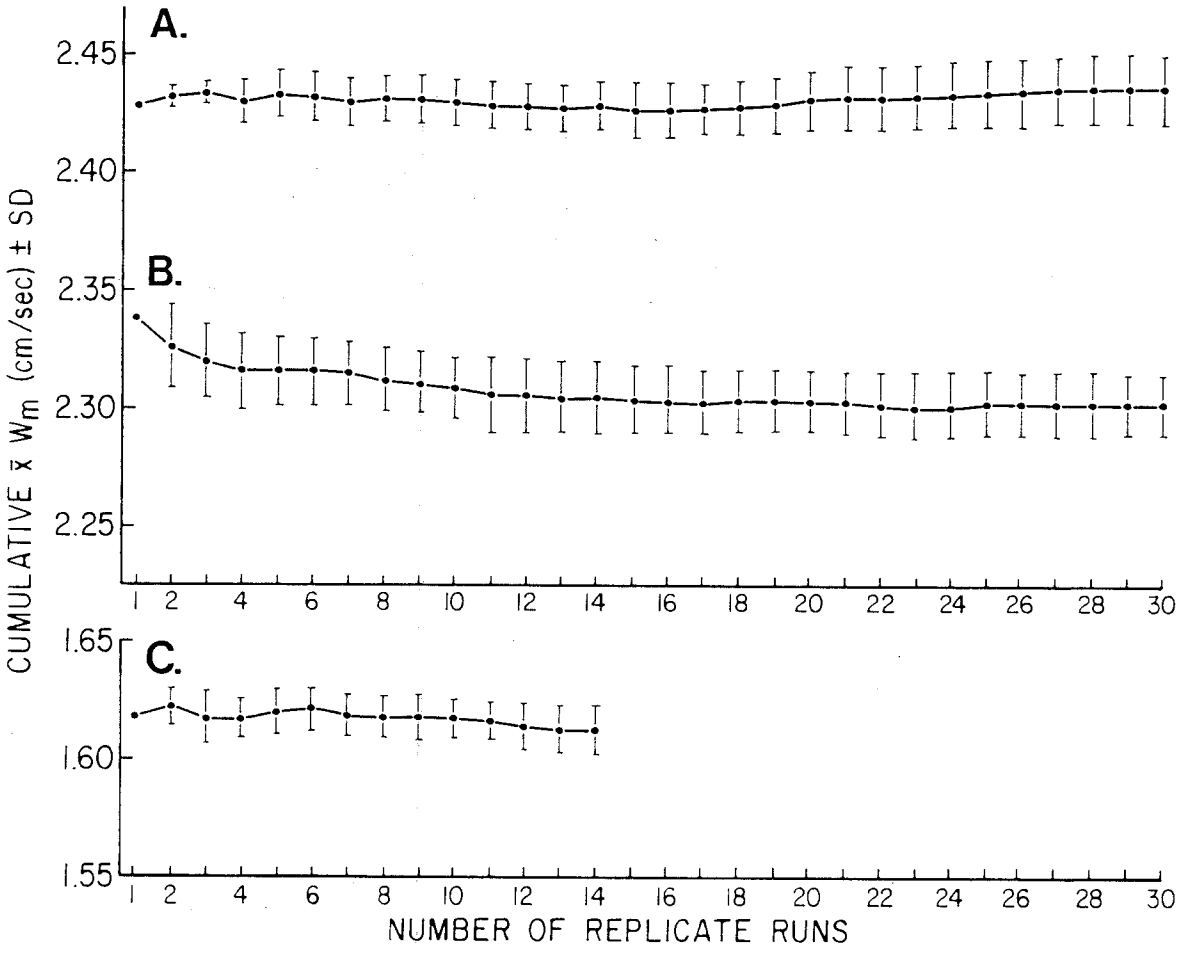


Figure 3.11: Relationship between the SD of replicate fall velocity measurements and the number of replicate runs for spherical particles tested in the large chamber. For line A the particle was a red plastic sphere (d = 514 ± 4 μm, ρ_p = 1.06 g/cm^3 but see also discussion in Section 3.4.1, this density value may be incorrect), for line B the particle was glass sphere (ρ_p = 2.42 g/cm^3, d = 230 ± 2 μm) and for line C the praticle was a glass sphere (ρ_p = 2.42 g/cm^3, d = 182 ± 2 μm). The mean water temperatures during all runs for a given particle were 13.8°C (line A) 13.1°C (line B), 12.7°C (line C). The values plotted are for runs timed over a vertical distance of 50 cm in the top half of the large chamber.

TABLE 3.5

Between-Runs Precision in the Small Chamber: Fall Velocities and Other Physical Characteristics of Spherical Particles[1]

ρ_p (g/cm^3)	d (μm)	Temperature range during runs (°C)	Number of replicate runs	W_m,[2] mean ± SD (cm/sec)	Percent CV	W_c[3] (cm/sec)	Percent difference in W_m and W_c[4]	R_p[5]
1.05	220	21.7 - 22.7	11	0.0644 ± 0.0065	10.0	0.0726	10.7	0.14
1.05	220	21.0 - 21.6	6	0.0689 ± 0.0030	4.4	0.0706	3.0	0.15
1.05	220	22.0	2	0.0566 ± 0.0038	6.6	0.0726	22.0	0.12
1.05	230	22.0 - 22.4	6	0.0707 ± 0.0043	6.0	0.0794	11.0	0.16

1. Described in Section 3.2.3.
2. Timed over a vertical distance of 25 cm.
3. Calculated from Stokes equation (see Section 3.2.7) with values of ρ_f and μ_f for the water temperature at the midpoint of the range listed in this table and a salinity of 32 ppt.
4. Calculated as a percentage of W_c.
5. Using d, W_m and values for ρ_f and μ_f as defined in footnote 3.

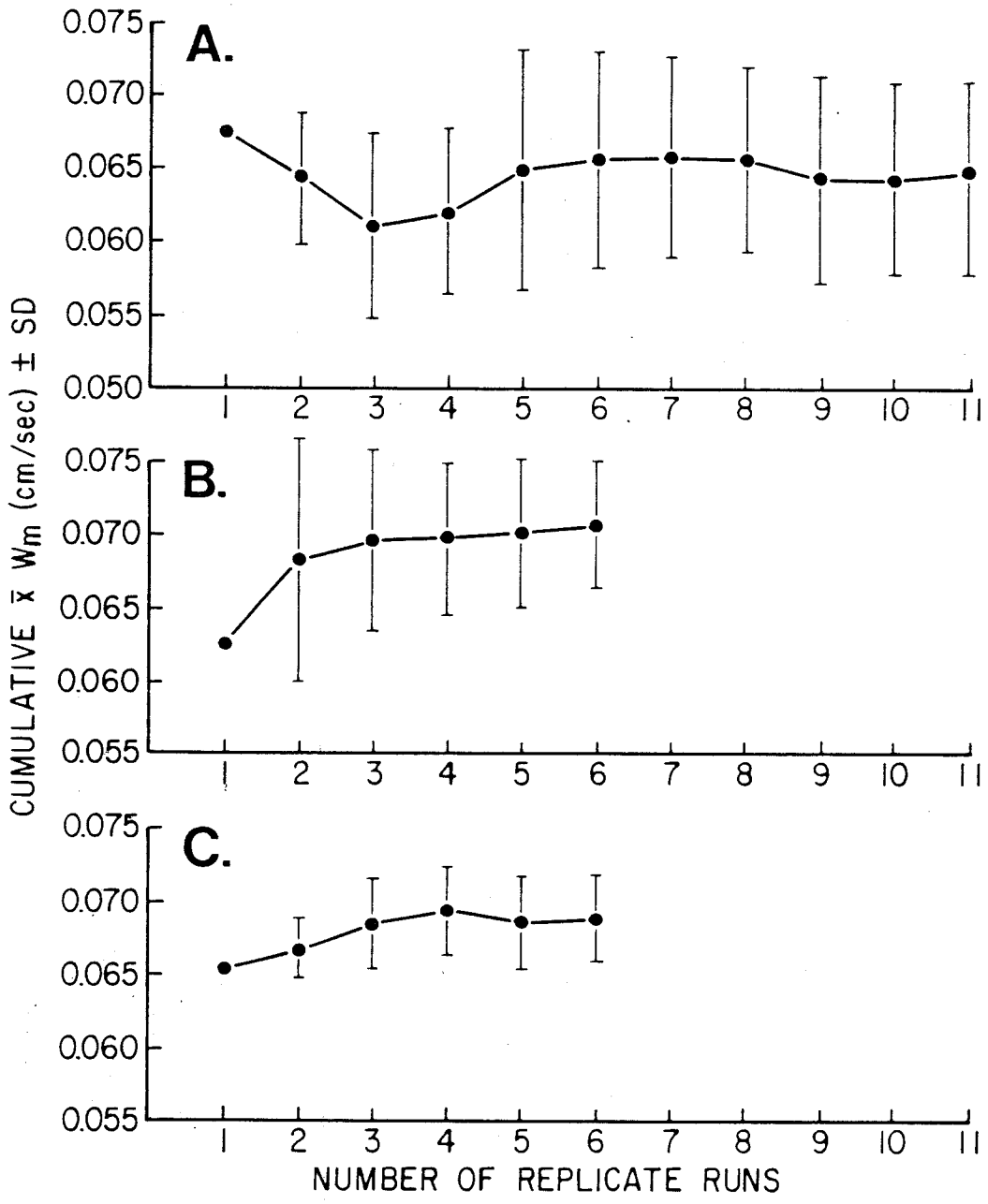


Figure 3.12: Relationship between the SD of replicate fall velocity measurements and the number of replicate runs for spherical particles tested in the small chamber. All particles were plastic spheres (ρ_p = 1.05 g/cm^3, d = 220 μm for lines A and C and d = 230 μm for line B). The mean water temperature during all runs for a given particle were 22.2°C (lines A and B) and 21.3°C (line C). The values plotted are for runs timed over a vertical distance of 25 cm.

(lines A and C, Figure 3.12), the mean W_m for the first run lies within the SD for all other runs. For the third sphere (middle line, Figure 3.12), the mean W_m for the first run is significantly (that is, outside one SD of the mean) lower than the mean for the last four runs. During a routine microscopic examination of the particle between runs, particulate material was observed on the surface of this third sphere between the first and second runs. This material was removed and did not reappear after subsequent runs. Thus, the particulate matter may have increased the drag of the sphere during the first run relative to other runs, causing the sphere to fall at a significantly slower speed.

Vertical profiles of W_m measured at successive intervals through the water column in the small chamber indicate that within-runs measurement precision for W_m averaged over 5-cm intervals is generally similar to the between-run measurement precision for W_m averaged over 25-cm intervals. Within-runs error (as estimated by CV for W_m from five contiguous 5-cm intervals during a single run) in 16 vertical profiles using four different spheres ranged from 0.6 to 12.3 percent. Of 11 runs with spheres using focused light, the percent CV ranged from 2.3 to 7.6 for nine runs and from 12.2 to 12.3 for two runs and of 14 runs conducted without focused light, the percent CV ranged from 0.6 to 4.9 for 13 runs and was 9.0 for the other run. A typical set of vertical profiles for six runs using the same sphere (Figure 3.13A) demonstrates that the locations in the water column of relative increases and decreases in W_m through a single profile varied

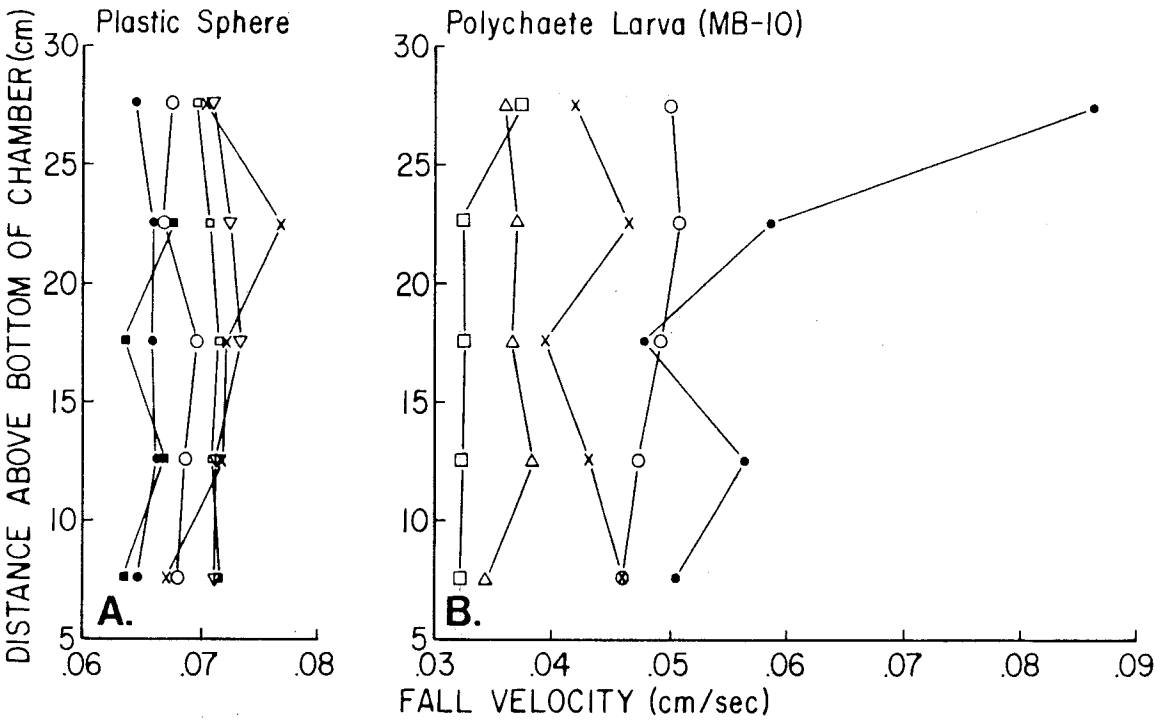


Figure 3.13: Profiles of 5-cm averaged fall velocities, measured in the small chamber, for a plastic sphere (A) and a polychaete larva (B). The fall velocities for contiguous 5-cm intervals during a single run (a total distance 25 cm and, in one case, 20 cm) are plotted here at the midpoint of each 5-cm interval. For the six runs using the plastic sphere (ρ = 1.05 g/cm^3, d = 220 μm), the time (EST) that each run began and the percent CV for the mean fall velocity during that run were, respectively, 13:25 and 1.4 percent (solid circles), 13:48 and 1.7 percent (open circles), 14:10 and 4.9 percent (crosses), 14:42 and 1.3 percent (open triangles), 15:04 and 3.1 percent (solid squares), 15:26 and 1.6 percent (open squares). The total range in water temperatures during all runs with this sphere was 21.0 to 21.3°C. For the five runs using the polychaete larva, MB-10 (described in Table 3.7), the total elapsed time since the narcotizing treatment (see Table 3.7) began and the percent CV for the mean fall velocity during that run were, respectively, 19 min and 25.7 percent (solid circles), 43 min and 4.2 percent (open circles), 64 min and 6.7 percent (crosses), 160 min and 3.9 percent (open triangles), 457 min and 6.7 percent (open squares). The total range in water temperature during all runs with this larva was 21.6 to 22.3°C.

haphazardly between profiles.

3.3.2 Fall velocities of polychaete larvae

Of the anesthetizing agents tested ($MgCl_2$, MS222, KCl, and Chloretone), all but $MgCl_2$ were effective in relaxing larvae for fall velocity measurements. Larvae continued to swim in all mixtures tested of $MgCl_2$ (7.3 percent, by weight, in distilled water) and seawater. Solutions of 2- to 3-ml MS222 (4 percent, by weight, in distilled water) and 10-ml seawater (final concentrations of 0.7 to 0.8 percent MS222, by weight) were used to narcotize most larvae (see Tables 3.6 and 3.7). A 58.3-percent Chloretone solution, by volume (7-ml saturated Chloretone solution in distilled water and 5-ml seawater), was used on seven Mission Bay Streblospio benedicti larvae and a 36.8-percent Chloretone solution was used to treat one MERL S. benedicti larva. Two KCl solutions, full strength 0.1-M KCl (mixed in distilled water) and a 0.33-percent KCl solution, by weight (11-ml 0.1-M KCl and 1-ml seawater), were each used once only, on MERL S. benedicti larvae.

The sequence of larval responses within a few minutes of immersion in the 0.7- to 0.8-percent MS222 solutions is described below. Reduction of active swimming behavior is the initial response; then the larvae, usually curled slightly (see Figure 3.1), sink to the bottom of the dish. The parapodia and setae usually point rearward, occassionally twitching at first; eventually the larvae lie motionless, except for the beating of cilia on the prostomium and pygidium. All cilial movements cease within a few minutes of immersion. The larvae usually secrete mucoid substances from their oral or aboral

TABLE 3.6

Fall Velocity During the First Run and Other Information About Each Polychaete Larva Tested in the Large Chamber

Polychaete[1] larva	NL[2] (μm)	NW[3] (μm)	Approximate[4] number of setigers	Treatment[5]	Treatment[6] interval (min)	Temp.[7] range (°C)	W_m [8] (cm/sec)	W_n [9] (cm/sec)
Eteone longa (Phyllodocid)	375	210	6	M7[10]	20	13.1-13.4	0.134[11]	0.160
Spionid- 1	885	383	NR[12]	M9	30	13.2-14.0	0.218	0.258
Spionid- 2	1400	313	17	M9	25	12.8-13.7	0.230	0.275
Spionid- 3	NR	NR	16	M8	40	11.3-11.4	0.142	0.179
Spionid- 4	1013	350	14-15	M8	23	10.6	0.199	0.256
				F	117 hr[13]	10.4	0.151	0.195
Spionid- 5	575	339	14-15	M8	10	10.8-10.9	0.158	0.201
Spionid- 6	NR	NR	18	M8	10	11.4-11.5	0.298	0.374
Spionid- 7	866	313	12-14	M8	15	10.7	0.091	0.117
Spionid- 8	976	350	12-13	M8	12	10.7	0.124	0.159
Spionid- 9	995	276	14	M8	21	10.6-10.7	0.184	0.236
Spionid-10	755	221	NR	M8	30	10.8-10.9	0.142	0.181

TABLE 3.6 (cont. - 2)

Polychaete[1] larva	NL[2] (μm)	NW[3] (μm)	Approximate[4] number of setigers	Treatment[5]	Treatment[6] interval (min)	Temp.[7] range (°C)	W_m [8] (cm/sec)	W_n [9] (cm/sec)
Spionid-11	755	332	NR	F[14]	5	10.5-10.6	0.218	0.304
Spionid-12	718	276	NR	F[14]	15	10.6-10.7	0.066	0.085
Spionid-13	1105	553	NR	E[14]	10	10.6-10.7	0.205	0.263
Spionid-14	NR	NR	NR	FW[15]	5	10.6-10.7	0.084	0.108

1. Larvae were collected in plankton tows (see Section 3.2.2) and identified to the lowest taxon possible.
2. See Figure 3.1.
3. See Figure 3.1.
4. Estimated from direct observations of the larvae.
5. Treatments desccribed in detail in Section 3.3.2; M7 = 0.7 percent MS222, M9 = 0.9 percent MS222, M8 = 0.8 percent MS222, F = 10 percent formalin, E = 80 percent ethanol, FW = freshwater.
6. Larvae were introduced into the water column immediately following treatment.
7. Temperature range throughout water column during time interval of first run.
8. Timed over a vertical distance of 50 cm in the top half of the large chamber, unless noted otherwise.
9. W_n = normalized fall velocity (defined in Section 3.3.2, eq. 3.7).
10. This larva was previously treated with 2.4 percent $MgCl_2$ solution for 30 min, with no apparent anesthetizing effect, and then transfered to the MS222 treatment.
11. Timed over a vertical distance of 50 cm in the bottom half of the large chamber.
12. NR = not recorded.
13. After the 0.8 percent MS222 treatment, this larva was settled repeatedly over a 3.5-hr interval (see Figure 3.14) and then fixed in 10 percent formalin. The larva remained in formalin for nearly 5 days (110 hrs) and then was transfered to seawater for a couple of minutes before it was introduced into the water column.
14. For all formalin and ethanol treatments, the larvae were rinsed in seawater after the treatment and prior to their introduction into the water column.
15. This larva extruded copious amounts of mucus and became very sticky while in the freshwater treatment. Initially the larva would not sink when introduced into the water column, but bobbed up to the surface; however, on the third introduction it did sink.

TABLE 3.7

Fall Velocity During the First Run and Other Information about each Polychaete Larva Tested in the Small Chamber

Polychaete[1] larva	NL[2] (μm)	NW[3] (μm)	Treatment[4]	Treatment interval (min)	Total[5] elapsed time (min)	Temp.[6] range (°C)	W_m [7] (cm/sec)	W_n [8] (cm/sec)
Brood A								
MERL-1 (11)	360	160	M4	20	27	20.1-20.4	0.0166 (5)	0.0167
Brood B								
MERL-2 (NR[9])	340	100	M7	11	40	22.0-22.6	0.0135 (15)	0.0129
MERL-3 (NR)	400	140	M4	10	63	22.0-22.6	0.0256 (20)	0.0245
MERL-4 (NR)	400	160	K	10[10]	52	22.0-23.1	0.0239	0.0228
MERL-5 (NR)	300	160	K33[11]	60[12]	137	22.0-23.1	0.0311	0.0296
			F	> 1 month[13]	22.2-22.4	0.0282	0.0270 (10)	
MERL-6 (NR)	NR	NR	C36	98[14]	135	22.0-22.4	0.0191	0.0184
Brood C								
MB- 1 (2)	400	160	M7	10	15	21.7-22.4	0.0641 (20)	0.0617
MB- 2 (2)	460	160	M7	11	29	21.7-22.4	0.0313 (20)	0.0301
MB- 3 (2)	360	200	M7	10	15	21.7-22.4	0.0530 (20)	0.0510

TABLE 3.7 (cont. - 2)

Polychaete[1] larva	NL[2] (μm)	NW[3] (μm)	Treatment[4]	Treatment interval (min)	Total[5] elapsed time (min)	Temp.[6] range (°C)	W_m [7] (cm/sec)	W_n [8] (cm/sec)
Brood C (cont.)								
MB- 4 (2)	440	140	M7	10	11	21.7-22.4	0.0464	0.0446
MB- 5 (2)	400	160	M7	10	15	21.7-22.4	0.0543	0.0522
Brood D								
MB- 6 (3)	360	200	M7	10	14	22.3-22.6	0.0421	0.0403
MB- 7 (3)	300	180	M7	15	10	22.3-22.6	0.0654	0.0626
MB- 8 (3)	320	160	M7	2	7	22.3-22.6	0.0603	0.0577
MB- 9 (6)	480-540	140	M7	10	15	21.1-21.6	0.0415	0.0407
Brood E								
MB-10 (1)	420-460	140	M7	10	19	21.6-21.8	0.0575	0.0559
MB-11 (1)	400-460	160	M7	10	15	21.6-22.1	0.0694	0.0671
MB-12 (1)	420	160	M7	10	21	21.6-22.1	0.0483	0.0467
MB-13 (2)	540	140	M7	10	15	21.6-22.3	0.0890	0.0856

TABLE 3.7 (cont. - 3)

Polychaete[1] larva	NL[2] (μm)	NW[3] (μm)	Treatment[4]	Treatment interval (min)	Total[5] elapsed time (min)	Temp.[6] range (°C)	W_m [7] (cm/sec)	W_n [8] (cm/sec)
Brood E (cont.)								
MB-14 (2)	480-580	180	C50	10	15	21.6-22.3	0.1150[15]	0.1106
MB-15 (2)	400-500	140	C58	10	15	21.6-22.3	0.0687	0.0661
MB-16 (2)	280-440	280	C58	10	15	21.6-22.3	0.0638	0.0614
MB-17 (2)	540-640	160	C58	10	18	21.6-22.3	0.0922[16]	0.0887
Brood F								
MB-18 (11)	540	100	C58	10	15	21.6-22.3	0.0423	0.0407
MB-19 (11)	540-560	100	C58	10	15	21.6-22.3	0.0408	0.0392
MB-20 (11)	640	100	C58	10	15	21.6-22.3	0.0355	0.0342

1. Larvae of the spionid polychaete, Streblospio benedicti were reared in the laboratory by Dr. Lisa A. Levin. Individuals are arranged here by brood. MERL = east coast larvae from the MERL tanks in RI (see Section 3.2.3); MB = west coast larvae from Mission Bay, CA (see Section 3.2.3); ( ) = age of larvae in days.
2. See Figure 3.1, larvae MB-9 through MB-20 were measured before and after each run. When a range in sizes is presented, it represents an increase in length due to the larvae uncurling during a run.
3. See Figure 3.1.

TABLE 3.7 (cont. - 4)

4. Treatments described in detail in Section 3.3.2; M4 = 0.4 percent MS222, M7 = 0.7 percent MS222, K = full strength 0.1-M KCl, K33 = 0.33 percent 0.1-M KCl, F = 10 percent formalin, C36 = 36.8 percent Chloretone, C50 = 50 percent Chloretone, C58 = 58.3 percent Chloretone.
5. At the time a larva was introduced into the water column, this is the total elapsed time since the treatment began. (Larvae were placed in seawater for several mins after each treatment and before introduction into the water column.)
6. Temperature range throughout water column during time interval of first run.
7. Timed over a vertical distance of 25 cm, unless noted as ( ) = vertical distance, in cm, of timed fall.
8. W_n = normalized fall velocity (defined in Section 3.3.2, eq. 3.7).
9. NR = not recorded.
10. On the day previous to this run, the larva was treated with a mixture of 0.1-M KCl and seawater, with no apparent anesthetizing effect. It was placed in seawater overnight and then treated as described here.
11. This treatment began as a mixture of 9-ml 0.1-M KCl and then more 0.1-M KCl was added to make the final 0.33 percent solution.
12. See footnote 11.
13. After treatment K33, this larva was settled twice over at ~ 3 hr interval and then fixed in 10 percent formalin. The larva remained in formalin for 35 days and then was transfered to seawater for a couple of mins before it was introduced into the water column.
14. The treatment began as a mixture of 6-ml seawater and 1-ml Chloretone (saturated solution) and then Chloretone was added to this mixture after the total elapsed times indicated: 1 ml after 9 min, 1 ml after 24 min, and 0.5 ml after 50 min.
15. The retrieved larva was beating its cilia and moving, so it may have been actively swimming or sinking during this first run. Thus, 22 min after the first treatment began, 2-ml Chloretone was added to the original treatment making a 58.3 percent Chloretone treatment. The mean W_m for this run was 0.0423 cm/sec.
16. The retrieved larva was twitching its body occassionally, but not beating its cilia.

ends. Larvae become very sticky in higher concentrations of MS222 or if immersed for long periods of time (> 30 min).

Larvae immersed in 0.7- to 0.8-percent MS222 for < 5 min usually revived in seawater, but after 5 to 10 min of immersion they did not revive. Lower concentrations (e.g., 0.4 percent) of MS222 required longer immersion times for movement to cease completely and then, sometimes, the larvae revived (e.g., began beating their cilia) during a fall velocity measurement.

The author was unable to find an anesthetizing procedure that maintained a nonswimming larva during the 20- to 30-min fall through seawater in one of the settling chambers and also permitted revival of the larvae after the fall. A procedure that completely narcotized a larva for the duration of its fall eventually killed the organism. Lower chemical concentrations or shorter immersion times resulted in larvae reviving at some point during their falls. Thus, the larvae were "narcotized to death" for all fall velocity measurements. However, the point at which actual physiological death took place in the organism is unclear (see Section 3.4.1).

Chloretone treatments resulted in larval responses similar to those described for MS222 treatments. However, in Chloretone larvae tended to curl up less than in MS222.

KCl solutions affected the larvae differently than the other narcotizing agents. In both the full-strength 0.1-M KCl and 0.33- percent 0.1-M KCl solutions, the larvae initially curled tightly into a ball and later uncurled completely to lie flat. The setae were splayed out to the sides in "fans," not pointing rearward

as in the MS222 and Chloretone treatments. In the full-strength 0.1-M KCl solution there were no external movements by the larva; however, fluid could be seen moving inside the organism indicating that it was still alive. In the 0.33-percent KCl solution the body, parapodia, and setae of the larva were motionless, but the cilia on the pygidium and prostomium continued to beat. In addition, fluid was observed moving inside the organism. These movements of KCl-treated larvae persisted even after the fall velocity measurements. However, one of the larvae eventually died; the larva treated with 0.33-percent KCl moved around in the dish after the fall velocity measurement but was dead by the next day. The larva treated with full-strength 0.1-M KCl was lost following its third run.

The most common orientation of larvae during their falls through either of the settling chambers was cup-shaped concave-up (see Figure 3.1). However, the larvae often rotated through other positions during a fall. Because relatively large (700-1400 μm) larvae were tested in the large chamber, the orientation of individuals relative to their local fall speed could be observed. These qualitative observations suggested that a larva fell fastest when falling head- first (refer to Figure 3.1 for diagrams of the orientations described), slowed down some in a cup-shaped concave-up or a tail-first orientation, and fell the slowest in a cup-shaped concave- down orientation or, for a noncurled individual, when the long axis of the larva was perpendicular to the velocity vector.

The fall velocity of larvae continually decreased with time since the larvae were first treated with an anesthetic (Figures 3.14 and

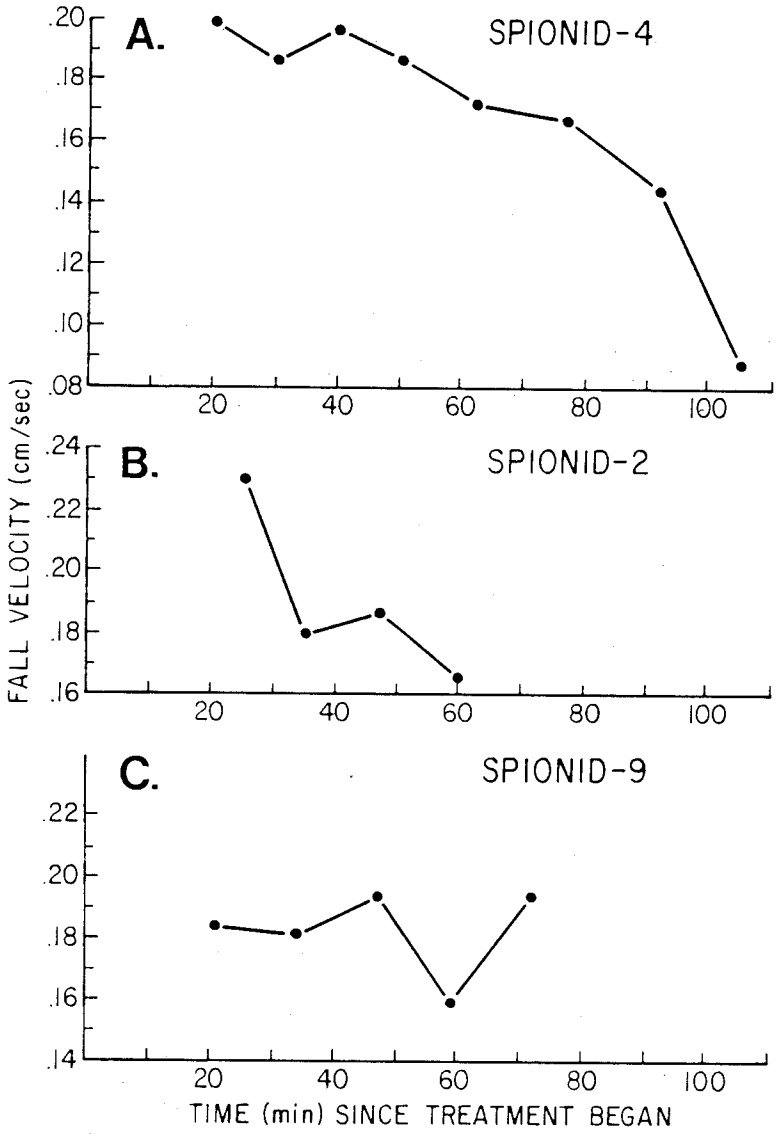


Figure 3.14: Relationship between fall velocity and time since anesthetizing treatment began for three spionids tested in the large chamber. The graphs are labeled with the individual tested; other information about these individuals is given in Table 3.6. Plotted here are fall velocities timed over a 50-cm interval in the top half of the large chamber. For the three graphs, the temperature range during all runs and the percent CV of all W_m values for the individual tested were, respectively, 10.6-10.9°C and 21.9 percent (Graph A), 12.5-13.7°C and 14.5 percent (Graph B), and 10.6-10.9°C and 7.9 percent (Graph C).

3.15) in about 70 percent of the larvae tested. Fall velocity also changed with time since the treatment began in the other 30 percent of the larvae tested, but the changes were not consistently in a particular direction (e.g., Spionid-9 in Figure 3.14 and MB-1 in Figure 3.15). The percent CV for fall velocities measured three or more times after a larva was narcotized ranged from 5.2 to 26.0 for 12 of the 13 individuals tested and was 39.5 for the other individual. Thus, only the fall velocities measured during the first run with each larva are presented here.

Within-runs variability in W_m was estimated for Streblospio benedicti larvae falling over contiguous 5-cm intervals in the small chamber. Initially, this variability was as high or higher than the between-runs variability: the percent CV was 3.2 to 18.5 for 16 runs and 21.8 to 40.4 for 14 runs. All of these runs were done in a dark room with a focused incandescent light shining directly into the water column to illuminate the larvae as they fall (see Section 3.2.3). When fall velocity measurements were made in a room with florescent ceiling lights and no focused light, the within-runs variability for 83 percent (20 out of 24) of the runs decreased by nearly a factor of two. For the 24 runs conducted in a lit room, the percent CV ranged from 1.6 to 9.7 for 17 runs, from 11.0 to 17.7 for three runs, and from 25.7 to 78.4 for four runs (characteristics of these last four runs are discussed in the next paragraph). An increase in within-runs measurement precision also occurred when fall velocity measurements of plastic spheres were made in a lit room without the focused light (see Section 3.3.1).

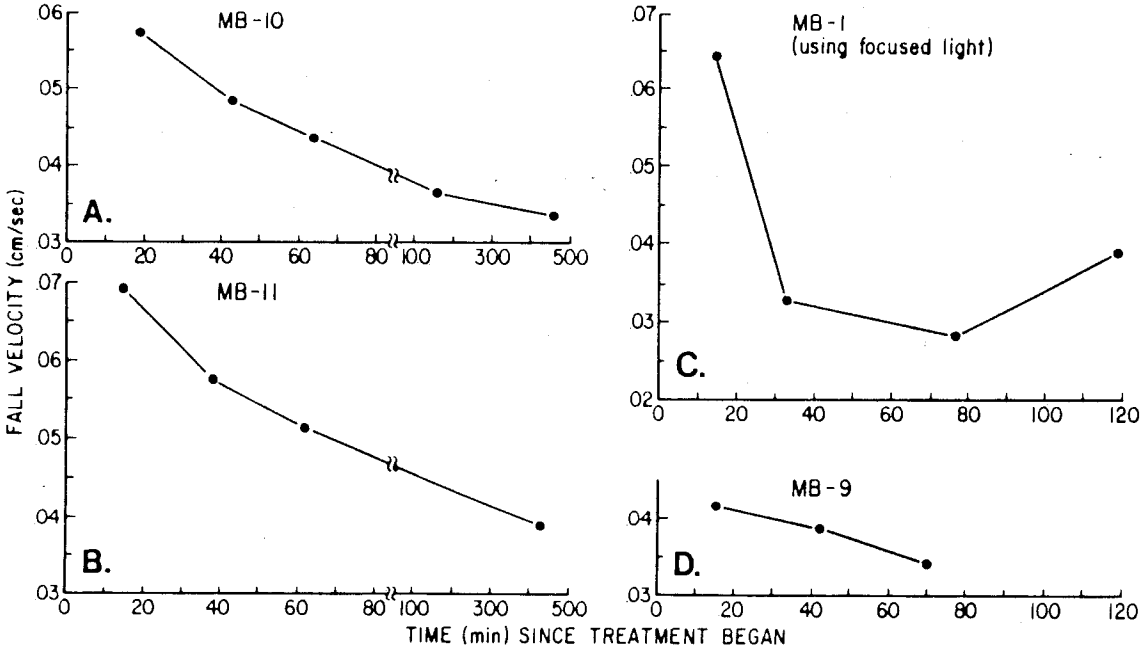


Figure 3.15: Relationship between fall velocity and time since anesthetizing treatment began for four Mission Bay Streblospio benedicti tested in the small chamber. The graphs are labeled with the individual tested; other information about these individuals is given in Table 3.7. All runs with MB-1 were made in a dark room using a focused light (see Section 3.2.3) and all runs with MB-9, MB-10, and MB-11 were done in a lit room without the focused light. Plotted here are 20-cm averaged fall velocities for MB-1 and 25-cm averaged fall velocities for MB-9, MB-10 and MB-11, except for the last run of MB-11 which was timed over only 15 cm. For the four graphs, the temperature range during all runs and the percent CV of all W_{fl} values for the individual tested were, respectively, 21.6-22.3°C and 22.2 percent (Graph A), 21.6-22.3°C and 23.7 percent (Graph B), and 21.7-22.4°C and 39.5 percent (Graph C), and 21.1-21.6°C and 9.7 percent (Graph D).

During the first-run measurements (conducted in a lit room), each of four Mission Bay Streblospio benedicti larvae fell considerably faster (the percent difference was 62 to 343 of the first run) through the 5-cm intervals in the upper water column than through the 5-cm intervals closer to the bottom (Table 3.8 and Figure 3.13B). Subsequent runs for MB-10, MB-13, and MB-14 yielded profiles of 5-cm averaged fall velocities similar to the "low W_m" (see Table 3.8 and Figure 3.13B) values measured in the first run. For example, ranges in W_m for the second runs (measured 38 to 43 min from the time the larvae were narcotized) were 0.0460-0.0501 cm/sec for MB-10, 0.0403-0.0596 cm/sec for MB-13 and 0.0411-0.0435 cm/sec for MB-14 (but see also footnote 15 on Table 3.7). MB-17 was not tested more than once. Two of the larvae (MB-14 and MB-17) showed signs of active movement upon routine microscopic examination of the larvae following the first run; MB-14 was actively beating some cilia while MB-17 was not beating any cilia but was twitching its body occassionally. The implications of these findings to the accuracy of the fall velocities measured in this study is discussed later (Section 3.4.1).

As previously discussed (Section 3.2.7), particle fall velocity is inversely related to fluid viscosity (see eq. 3.5). Seawater viscosity increases only slightly with relatively large increases in salinity; at 20°C, μ_f increases from 1.07×10^{-2} g/(cm)(sec) for 35 ppt water or by only 1.9 percent for a 16.7 percent increase in salinity. Seawater salinities varied by only ~ 2 ppt in this study: salinities in the large chamber ranged from 30.4 to 31.4 ppt, in the

TABLE 3.8

Relationship Between 5-cm Averaged Fall Velocities and Distance above Bottom of Small Chamber During the First Runs for Four Mission Bay *Streblospio benedicti* Larvae[1]

5-cm interval above bottom of chamber	*Streblospio benedicti* larva[2] MB-10	MB-13	MB-14	MB-17
30-25 cm	0.0865*	0.2524*	0.2990*	0.2979*
25-20 cm	0.0587	0.2334*	0.2612*	0.1185*
20-15 cm	0.0479	0.1578*	0.2567*	0.0685
15-10 cm	0.0565	0.0440	0.2212*	0.0706
10- 5 cm	0.0505	0.0529	0.0600	0.0729
Average High W_m (marked with *)	0.0865	0.2146	0.2595	0.2082
Average low W_m	0.0534	0.0484	0.0600	0.0707
Percent Difference[3]	62	343	332	194

1. Values of W_m for the 5-cm interval indicated are listed in this table.
2. Other characteristics of these larvae are given in Table 3.7.
3. Calculated as $\frac{\text{Mean High } W_m - \text{Mean Low } W_m}{\text{Mean Low } W_m} \times 100$.

small chamber from 31.5 to 32.5 ppt and in the field from 30.9 to 31.7 ppt (L.K. Rosenfeld, personal communication). However, seawater viscosity is much more sensitive to changes in water temperature for the range that occurred during this study. The viscosity of 30 ppt seawater increases from ~ 1.00×10^{-2} g/(cm)(sec) at 23°C to ~ 1.38×10^{-2} g/(cm)(sec) at 10°C or by about 38 percent. Fall velocities of larvae were measured over a temperature range of 10.4 to 14.0°C in the large chamber and of 21.0 to 23.1°C in the small chamber. The mean water temperature during the trap collecting intervals in the field ranged from 18.9 to 21.9°C (see Table 4.4). To correct for the variability in water viscosity in laboratory measurements and in the field environment, normalized fall velocities (W_n) were calculated as

$$W_n = W_m \left(\frac{\mu_{f\text{-}lab}}{\mu_{f\text{-}field}}\right) \tag{3.7}$$

where $\mu_{f\text{-}lab}$ = the water viscosity of 30 ppt seawater for the water temperature at the midpoint of the range measured during the course of the fall velocity measurements (see Tables 3.6 and 3.7) and $\mu_{f\text{-}field}$ = the water viscosity of 1.055×10^{-2} g/(cm)(sec) for 30-ppt seawater at 20.4°C (the midpoint of the range of the mean water temperature measured during the trap collections in the field).

In the large chamber, fall velocities were measured for 14 spionid larvae and one phyllodocid (Eteone longa) larva, all larvae ranging from 375 to 1400 μm in narcotized length (see Figure 3.1). The normalized fall velocities (W_n) of larvae treated with MS222

were 0.160 to 0.374 cm/sec; for larvae killed in formalin, ethanol or freshwater, W_n = 0.085-0.263 cm/sec (Table 3.6). Fall velocity is positively correlated with narcotized length (Figure 3.16); r_s (the Spearman rank correlation coefficient) is 0.58 for larvae treated with MS222 (N = 9) and r_s is 0.54 if the larvae killed in formalin and ethanol are included (N = 12); for both r_s values, the H_o of no correlation between the parameters can be rejected at $\alpha \leq 0.05$.

In the small chamber, fall velocities were measured for six MERL Strebeospio benedicti (five from one brood and one from another) and for 20 Mission Bay Strebeospio benedicti larvae from four broods (see Table 3.7). The larvae ranged from 300 to 640 μm in narcotized length. Normalized fall velocity (W_n) ranges for larvae treated with MS222 were from 0.0129 to 0.0856 cm/sec (N = 16), for larvae treated with Chloretone W_n = 0.0184-0.1106 cm/sec (N = 8), for larvae treated with KCl W_n = 0.0228-0.0296 cm/sec (N = 2) and for the one individual (MERL-5) fixed in formalin after treatment with KCl, W_n = 0.0270 (Table 3.7). Normalized fall velocity was not significantly correlated with narcotized length (r_s = 0.14, H_o could not be rejected at $\alpha \leq 0.05$, and see Figure 3.16) for the 25 larvae tested in the small chamber. However, narcotized lengths of larvae tested in the small chamber spanned a relatively small range (340 μm) compared to larvae tested in the large chamber (spanning a narcotized length range of 1025 μm). A positive correlation between W_n and narcotized length was strongest (r_s = 0.65, H_o rejected at $\alpha \leq 0.01$) if values of W_n for all larvae tested in both chambers are included in the analysis.

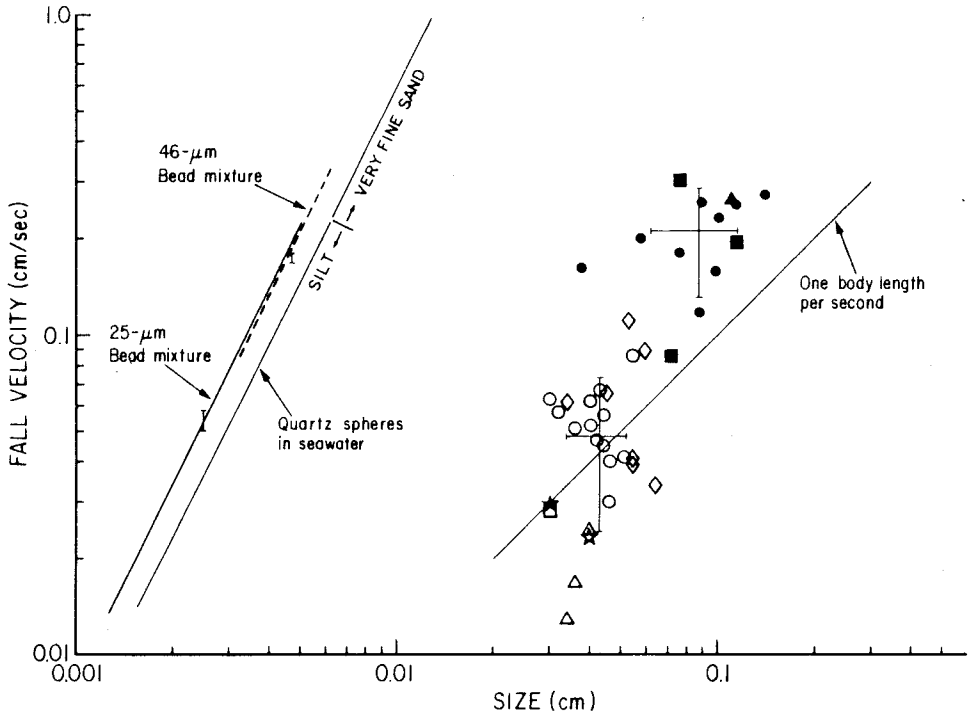


Figure 3.16: Relationship between fall velocity and size for all larvae tested, for the glass bead mixtures used in the flume, and for quartz spheres. For larvae, the narcotized lengths (NL) and measured W_n values listed in Tables 3.6 and 3.7 are plotted here. Values are plotted for the following Streblospio benedicti larvae tested in the small chamber: Mission Bay larvae treated with MS222 (open triangles), with KCl (stars), with formalin (open square) and MERL larvae treated with MS222 (open circles), with Chloretone (open diamonds), and for the following spionid (and one Eteone longa) larvae tested in the large chamber: larvae treated with MS222 (solid circles), with formalin (solid squares), and with ethanol (solid triangle). The mean W_n (± SD) and mean NL (± SD) are plotted separately amongst all larvae tested in the small chamber and all larvae tested in the large chamber. A solid line through the larval fall velocity plot depicts the one body length per second fall velocity versus size relationship described by Rudyakov and Tseytlin (1980). The calculated fall velocities (in freshwater, atmospheric pressure, 24°C) for the range in sizes (bead diameter) and fall velocities of ~ 94 percent of the beads in the 25-μm mixture (solid line) and of ~ 97 percent of the beads in the 46-μm mixture (dotted line). Plotted as vertical bars are the ranges of W_c for a 24.8-μm bead falling through 22°C to 28°C freshwater (atmospheric pressure) and for a 46.4-μm bead falling through 20°C to 23°C freshwater (atmospheric pressure). The calculated fall velocities of quartz (ρ_p = 2.65 g/cm^3) spheres falling through 30 ppt seawater at 20.45°C (atmospheric pressure) is plotted versus particle diameter as a solid line. Classification of these particles as "silt" or "very fine sand" is also shown on the Figure.

Because the fall velocities of larvae settled in the small chamber are essentially independent of narcotized body length, it is possible to pool all larval sizes for further statistical analyses. Statistical tests of the effects on fall velocity estimates of paternal origin (east or west coast), genetic affinity (brood), treatment, and larval age are discussed below.

The east coast Streblospio benedicti (from the MERL tanks) larvae fell more slowly than the west coast (Mission Bay) S. benedicti larvae. All fall velocities measured for MERL larvae were lower than the fall velocities measured for Mission Bay larvae; W_n ranged from 0.0129 to 0.0296 cm/sec for the MERL larvae and from 0.0301 to 0.1106 cm/sec for the Mission Bay larvae. The morphological differences between east and west coast populations of this species may contribute to these differences in fall velocity; the east coast larvae possess long swimming setae while the west coast larvae do not. These swimming setae may increase the drag on a larva, causing it to fall more slowly relative to a larva without swimming setae. Alternatively, the differences in fall velocity may be due to the total elapsed time between when a treatment began and when the larvae were tested in the chamber (see Section 3.4.1) or to the age of the larvae at the time they were tested in the chamber (see below).

If there is a larval age effect, it apparently results in a decreased fall velocity with increasing age. A test of the H_o that there is no difference between the fall velocity of two day-old and 11 day-old larvae was made for the Chloretone-treated larvae from Mission Bay in Broods E and F (see Table 3.7). In this comparison,

the H_0 could be rejected at $\alpha \leq 0.057$ or 0.028 (the actual value of α depends on how the tied values are treated in the Mann-Whitney U test, see Siegel 1956, pages 116-127). Because 11 day-old Mission Bay larvae have significantly lower fall velocities than two day-old Mission Bay larvae, it is possible that 11 day-old MERL larvae also have relatively low W_n. Unfortunately, of the seven MERL larvae tested, the age of only one individual was known (see Table 3.7).

Genetic affinity did not have a significant effect on the fall velocity of one to six day-old larvae from Mission Bay (Broods C, D, and E, all treated with MS222; see Table 3.7). The H_0 that there is no difference in fall velocity between the broods could not be rejected, even at $\alpha \leq 0.102$, using the Kruskal-Wallis test.

A visual inspection of the fall velocity data plotted in Figure 3.16 indicates that the variability in fall velocity estimates for all larvae treated with MS222 encompasses the fall velocity estimates for larvae treated otherwise (with KCl, Chloretone, formalin, or ethanol). Statistical analyses of these data were limited by the small sample sizes for most of the alternative treatments. However, a statistical test of the H_0 that there is no difference in fall velocity due to a treatment effect could be made for the Mission Bay larvae from Brood E, where half of the individuals were treated with MS222 and half with Chloretone (see Table 3.7). In this comparison, the H_0 could be rejected only at $\alpha \leq 0.171$ (Mann-Whitney U test); thus, the H_0 was accepted. Again, the possibility that a larval age effect obscures real differences between treatments is discussed later (Section 3.4.1).

3.3.3 The flume flow regime

While velocity profiles of the flume flow were not possible (see Section 3.2.4), the structure of the flow regime at the test section was visualized using dye. Photographs of dye released from a probe positioned at distances of approximately 40-, 50-, 60-, and 70-cm above the bottom (Figure 3.17) clearly show a turbulent flow regime. The relatively regular vortices immediately downstream of the probe were an artifact of the flow visualization technique and do not represent the turbulence in the oncoming flow. The cylindrical probe sufficiently disturbed the flow so that vortices were shed in the wake of the cylinder. However, in laminar flow, a regular dynamic structure to these vortices would persist in the downstream direction until parallel streamlines were eventually restored by the viscous forces in the flow. The dye would spread vertically or cross-stream only due to diffusion. In the flume flow pictured here (Figure 3.17) turbulent eddies distort the vortex structure downstream of the probe. Eddies of various sizes can be seen spreading the dye vertically (see especially Figure 3.17D). This background turbulence in the oncoming flow probably results from the flume design, i.e., the manner in which water is supplied to the flume through the diffuser (see Section 3.2.4).

Measured flow speeds in the flume (Table 3.9) also reflect the turbulent nature of the flume flow. Although the centrifugal pump was always set at the maximum pumping rate, instantaneous flow speeds (read every 10 sec) varied between 8 and 12 cm/sec. However, the mean flow speed during six 4- to 16-min intervals varied only by

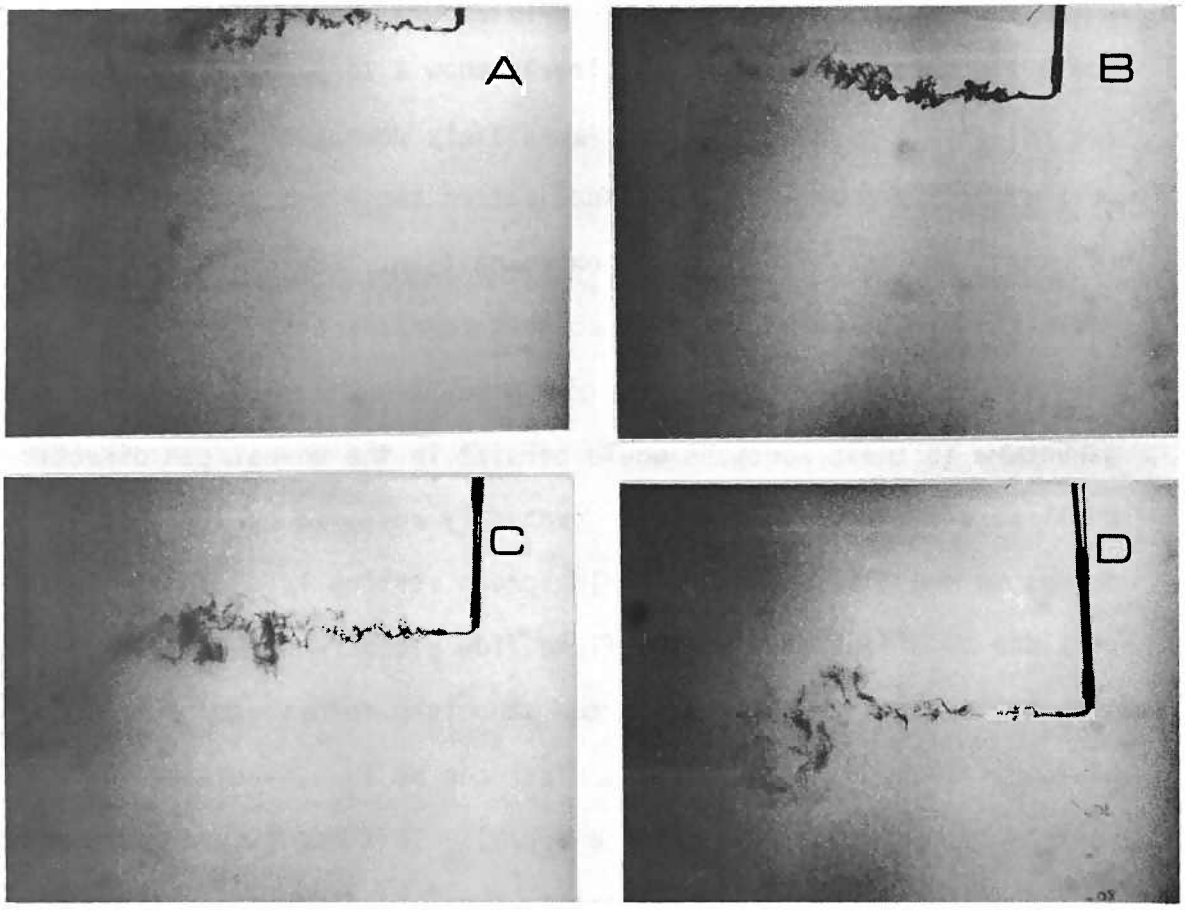


Figure 3.17: Visualization, using dye, of the turbulent structure of the flume flow regime. Dye (blue food coloring) mixed with freshwater was placed in a bucket of flume water during experiments to maintain the dye solution at the flume water temperature (11 to 12°C in these experiments). The dye solution entered the probe by a manually operated gravity feed. During this dye study the flume was filled with water to a height of ~ 75 cm; the centrifugal pump was operated at the maximum pumping rate. Probe was ~ 70-cm (A), ~ 60-cm (B), ~ 50-cm (C), and ~ 40-cm (D) above the flume bottom.

TABLE 3.9

Measured Flume Flow Speeds During Two Series of Trap Tests

Approx. Time Interval (min)	Number of Readings[1]	Measured Flow Speed (cm/sec) Range	Mean	SD	Percent CV	Approx. Flume Water Height (cm)
6/24/82 SERIES						
16	98	9-12	11.0	0.8	7.3	68.5
4	25	9-12	11.0	0.9	8.2	67.5
8	52	10-12	11.1	0.7	6.3	67.0
6	40	9-12	10.6	0.8	7.5	67.0
7/22/82 SERIES						
10	55	8-11	10.1	0.7	6.9	73.5
10	61	9-12	10.3	0.6	5.8	70.5

1. A reading was taken every 10 sec during the approximate time intervals listed here.

1.0 cm/sec, ranging from 10.1 to 11.1 cm/sec. The variability in mean flow speeds between intervals is due to, (1) the measurement characteristics of the electromagnetic current meter, (2) the number of readings used to calculate each mean and (3) the flume water height during the measurements. By conservation of mass, a mean flow speed for any given flume water height can be used to predict the flow speed for any other height (see caption to Figure 3.18) as long as the flow speed is constant. Using the measured flow speed over the longest time interval (i.e., for the largest number of readings, see Table 3.9), mean flow speeds for flume water heights from 50 to 75 cm/sec were calculated (Figure 3.18). All measured mean flow speeds lie within the error bars of these calculated flows.

Calculated mean flow speeds during trap tests differed by a maximum of only 2.3 cm/sec (see Figure 3.18 for flume water heights listed in Table 3.10). This variability is insignificant given that the measured flow speeds usually spanned a range of 4 cm/sec and the error bars around these means were 6 to 8 percent ($\simeq$ 1 cm/sec). Furthermore, mean flow speeds varied by a maximum of only 1.0 cm/sec for all trap tests using the 25-μm bead mixture (for these series, flume water heights varied between 68.5 and 75 cm, see Table 3.10). The calculated mean flume flow speed was significantly higher (by up to 4.7 cm/sec) during the series where water sampling methods were compared (see Table 3.10) because the flume was filled only to 51-52 cm. However, results of the methods comparison are supported by theoretical arguments that would also apply to slightly higher flume flows (see Section 3.2.5).

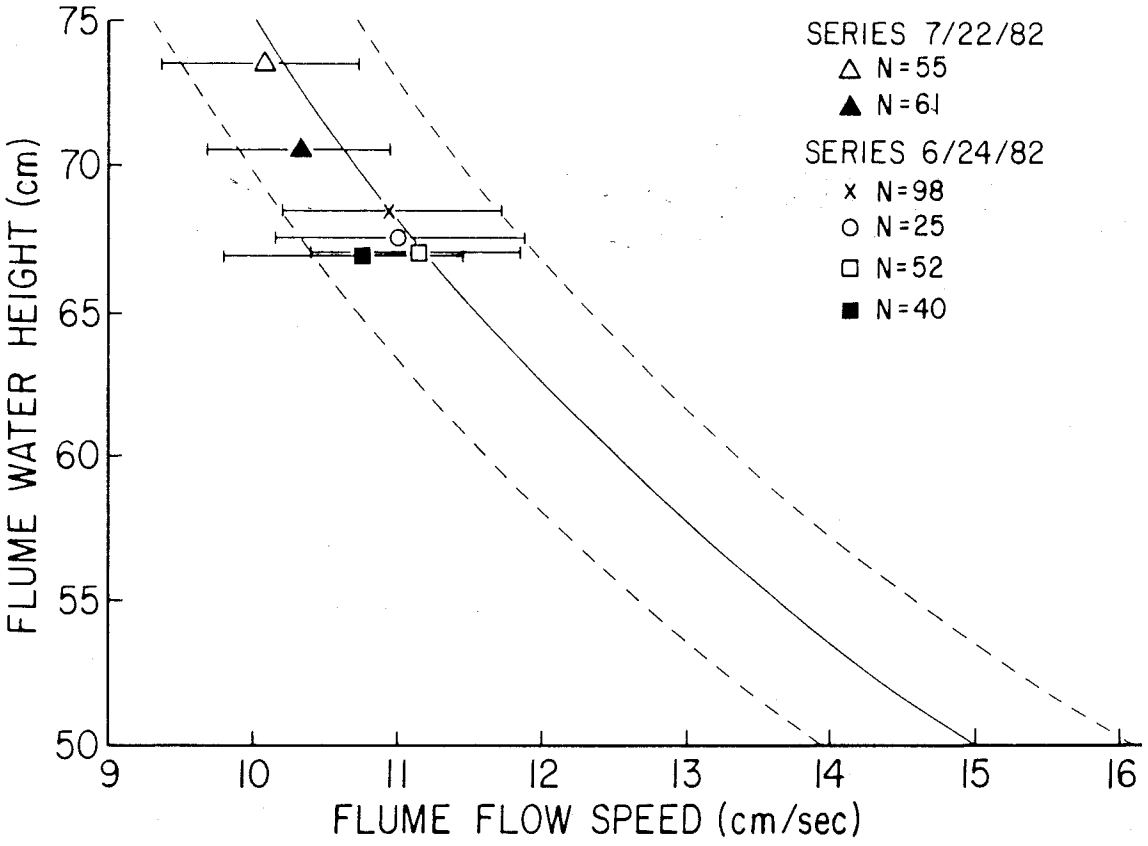


Figure 3.18: Calculated and measured flume flow speeds at the maximum pumping rate for flume water heights of 50 to 75 cm. The values were calculated as: $V_2 = V_1 H_1/H_2$, where V_1 = the mean measured flow speed for the largest number of readings (98 readings taken over a 16-min interval, see Table 3.10), H_1 = flume water height during the 16-min interval (note that flume width was a constant 61 cm during all series so it cancelled out in conservation of mass calculations), V_2 = calculated mean flow speed (solid line in the Figure) for a new flume water height, H_2. The dotted line in the Figure represents error bars of ~ 7 percent around the mean (see Table 3.10). The measured mean and SD values listed in Table 3.10 are also plotted on the Figure.

The technique for seeding the flow with beads coupled with the turbulence in the flow provided a well-mixed water mass to the test section. Vertical profiles of bead concentrations taken near the beginning, midpoint and end of each series (Figure 3.19) show random oscillations in bead concentrations with respect to sample height. The water column was well-mixed for particle concentrations from 3 to 15 mg/l. The mean CV for the profiles was 6.1 percent (SD = 2.9 percent, range = 2.1-13.1 percent), well within the range in CV for particle concentrations taken over 8.5 min intervals at a single depth (see Appendix III).

To statistically test for an even distribution in particle concentrations with distance above the bottom, all samples taken at a given depth were treated as replicates. Only the nine profiles where paired water samples were collected at all six depths were included in the analysis; the profiles excluded were all profiles during both the 5/25-5/26/82 and 6/7/82 series, the midpoint profile during 8/24/82 series, and the first profile during both the 7/10/82 and 6/24/82 series. If the water column is well-mixed, then the variability in particle concentrations at each depth should be similar. This H_0 could not be rejected at $\alpha \leq 0.05$ (in fact, it could not be rejected even at $\alpha \leq 0.99$) using the nonparametric Kruskal-Wallis test.

The maximum difference in bead concentrations during a given series of trap tests ranged from 3.5 to 6.5 mg/l (see last column of Table 3.10). Concentrations gradually increased and decreased over each series because of difficulties in maintaining a constant rate

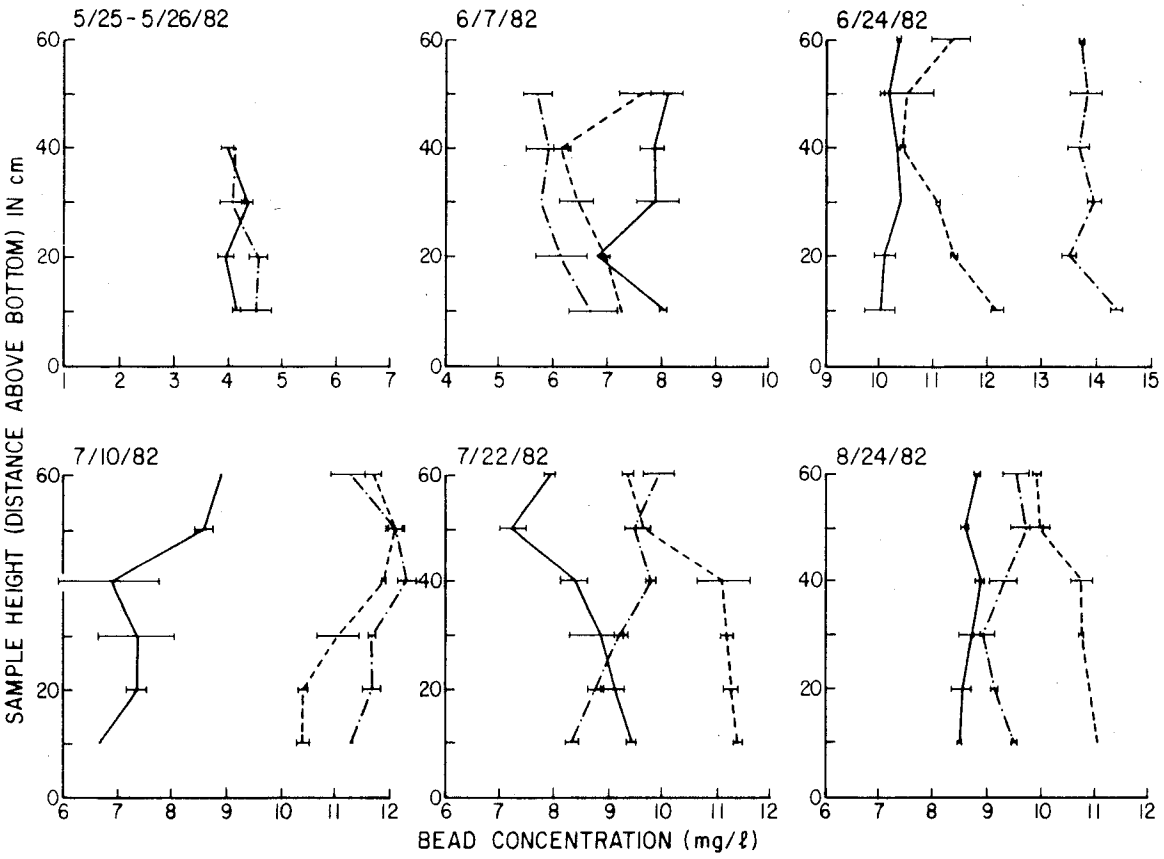


Figure 3.19: Vertical profiles of bead concentrations at the test section during all series. Horizontal bars connect the range in values for the paired water samples taken at each depth. Mean concentrations are connected by a solid line for the profile taken near the beginning of a series, by a dashed line for the midpoint profile, and by a dot-and-dashed line for the profile taken near the end of the series. For all series except 5/25-5/26/82, the mean background particle concentrations for each series (listed in Table 3.10) were subtracted from the measured bead concentration.

for supplying the flume with the bead tank suspension (see also Section 3.2.5). The changes in concentration were always gradual ($\leq$ 0.10 mg/l per min).

3.3.4 Effect of the length of the trap collecting interval on relative particle collection efficiency

The effect of the length of the trap collecting interval on the relative collection efficiencies of five trap designs was tested during the 6/7/82 and 6/24/82 series. Traps OPC8.5-2.7, OPC8.5-1.9 OPC8.5-1.0, and OPF8.5-1.9 were each tested for intervals of 4.5, 6.5 and 8.5 min during the 6/7/82 series. Traps OPC8.5-2.7 and OPC8.5-3.6 were each tested for intervals of 4.5, 6.5, 8.5 and 16.5 min during the 6/24/82 series.

Results of these tests indicate that collections by all of the trap designs probably reached steady state within 4.5 min. For all trap designs tested in the 6/7/82 series, relative particle collection efficiencies did not differ significantly between the three trap collecting intervals (Figure 3.20). The H_0 that collection efficiency does not vary with the length of the trap collecting interval could not be rejected at $\alpha \leq 0.05$ (using the Kruskal-Wallis test) in separate tests for each of the four trap designs.

However, for the largest trap volume tested during the 6/7/82 series, trap OPC8.5-2.7, there was a slight trend of increasing particle collection efficiency with increasing length of the trap collecting interval (see top graph in Figure 3.20). This result stimulated tests of an even longer trap collecting interval (16.5 min), along with a larger-volume trap (OPC8.5-3.6) during the

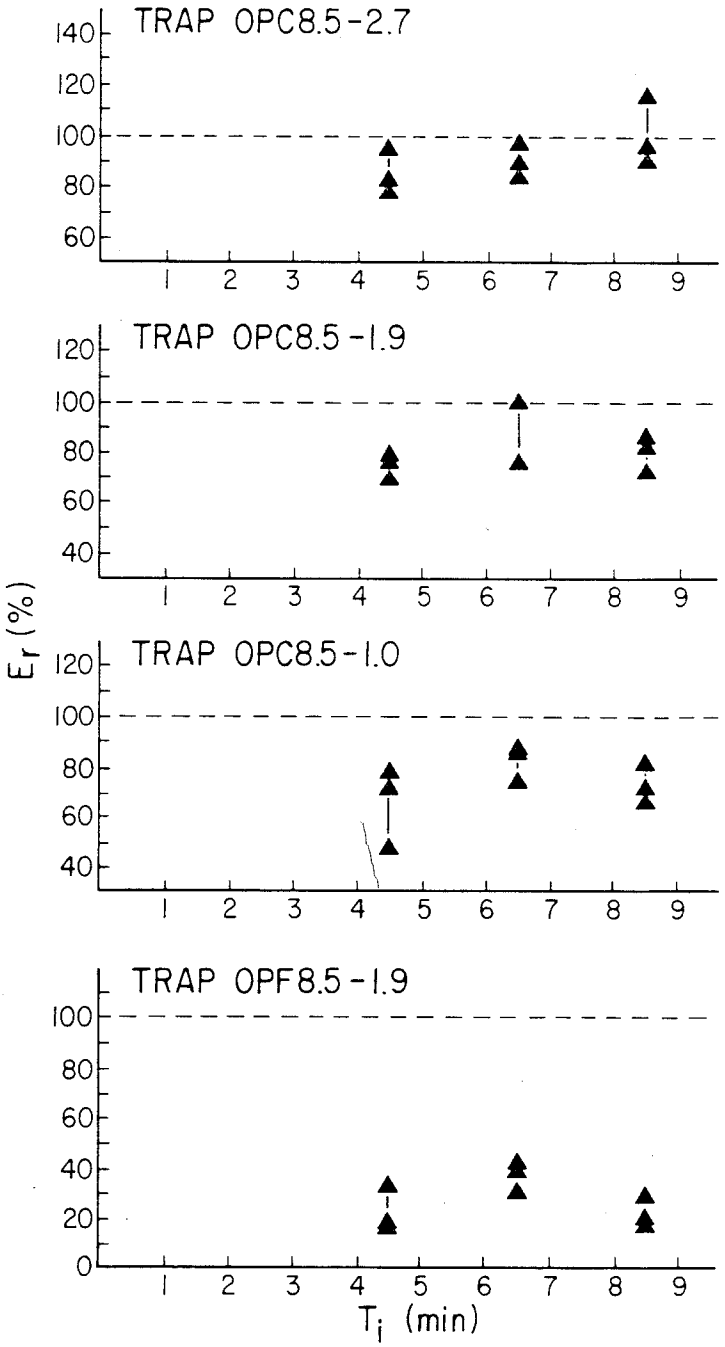


Figure 3.20: Relative particle collection efficiencies of four trap designs, each tested for trap collecting intervals of 4.5, 6.5 and 8.5 min during the 6/7/82 series. Conditions during this series are given in Table 3.10 and the raw data for the E_r values plotted here are listed in Appendix III.

6/24/82 series. For these trap tests (see Figure 3.21), the H_o of no difference in collection efficiency between trap collecting intervals was tested against the a priori ordered H_a that particle collection efficiency increases for longer trap collecting intervals (using the Jonckheere test). For separate statistical tests of both trap designs, this H_o could not be rejected at $\alpha \leq 0.0515$, or even at $\alpha \leq 0.5276$.

For the remainder of the series, a trap collecting interval of 8.5 min was selected as a compromise value that maximized the weight of particles collected by the smallest trap to be tested (trap TBC1.7-3.0, see Table 3.1), while minimizing the variability in particle concentration over the collecting interval (for the nine 8.5-min intervals in the 6/24/82 series, the CV for C_i ranged from 3.9 to 8.3 percent, mean = 5.3 ± 1.5 percent, but for the six 16.5-min intervals, CV ranged from 2.6 to 15.3 percent, mean = 7.4 ± 4.5 percent). The subsequent series also were conducted with all trap mouths 47- or 51-cm above the bottom (compared with 34-cm above the bottom in the 6/7/82 and 6/24/82 series, see Table 3.10). These heights were dictated by the height of the largest trap to be tested during a given series. The total height of trap TBC14.7-2.9 was 47 cm (including the basket and the pedastal, see Section 3.2.6) in the 7/10/82 series, however, this arrangement was unsuccessful; the successful arrangement used in the 7/22/82 and 8/24/82 series was 51-cm tall. To determine if particle collection efficiencies differ when trap mouths are at heights of 34- versus 47-cm above the bottom, trap OPC8.5-2.7 was tested at both heights

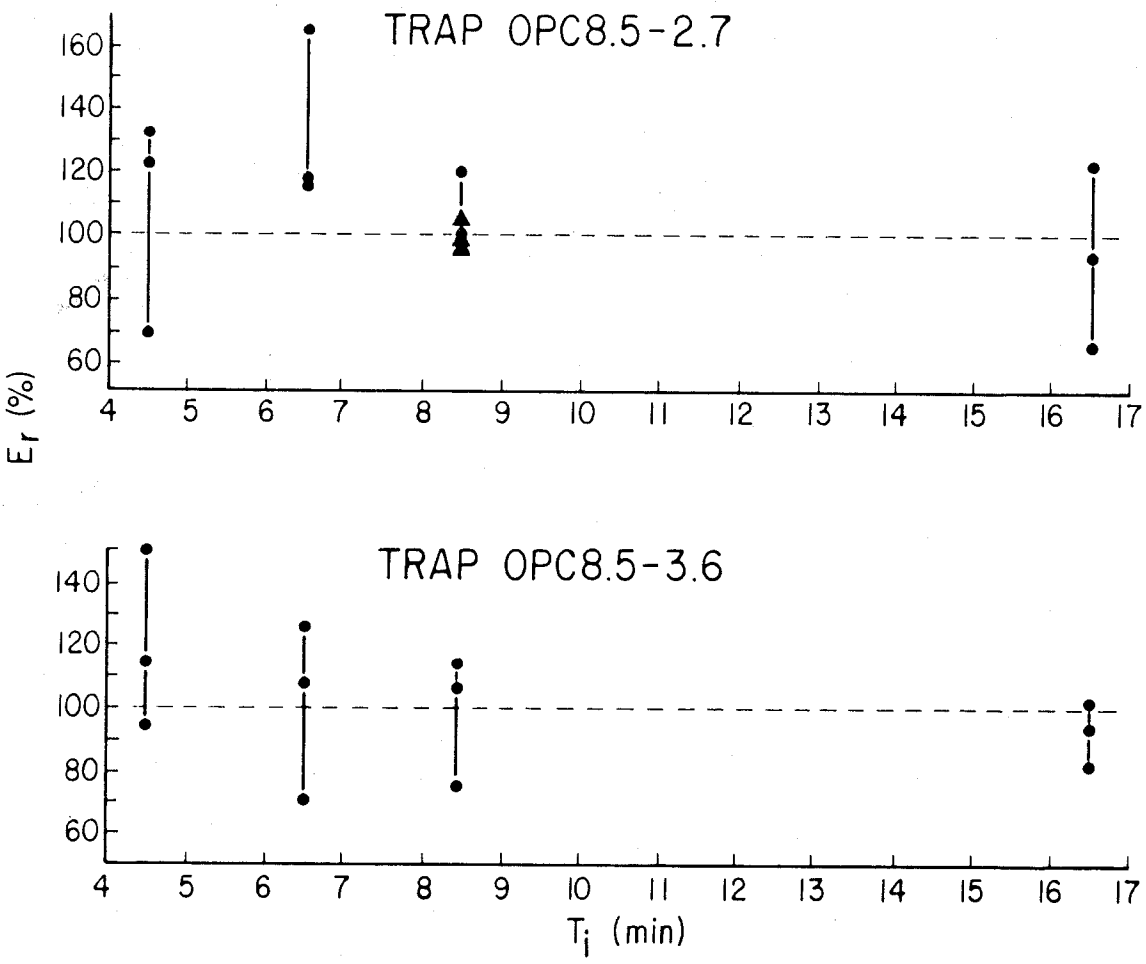


Figure 3.21: Relative particle collection efficiencies of two trap designs, each tested for trap collecting intervals of 4.5, 6.5, 8.5 and 16.5 min during the 6/24/82 series. For all of the collecting intervals, trap mouths of both trap designs were positioned 34-cm above the bottom. In addition, three replicates of trap OPC8.5-2.7, collecting for 8.5 min, were positioned 47-cm above the bottom (these replicates are indicated as solid triangles on the figure). The mean particle collection efficiency for these three replicates, and not the three replicates positioned 34-cm above the bottom, of trap OPC8.5-3.7 was used as the normalizing factor, E_s, during this series (see Appendix III). Conditions during this series are given in Table 3.10 and the raw data for the E_r values plotted here are listed in Appendix III.

during the 8.5-min intervals of the 6/24/82 series (see Figure 3.21). The H_o that collection efficiency does not differ with height of the trap mouth above the bottom could not be rejected at $\alpha \leq 0.050$ (using the Mann-Whitney U test).

3.3.5 Particle collection efficiencies of a single trap design tested in all of the series

Trap OPC8.5-2.7 was tested during each series; the mean particle collection efficiency of this trap during a given series was used as the normalizing factor, E_s, for calculations of E_r during that series (see Section 3.2.7). These normalizations of the data were necessary because the ranges in replicate efficiencies (E) of this trap varied between series (see Figure 3.22). For the series where unsonicated 25-μm bead mixtures were used to seed the flow (series 6/24/82, 7/10/82 and 7/22/82), the ranges in replicate particle collection efficiencies overlapped among the three series; however, collection efficiencies tended to be higher in the 7/22/82 than in the other two series. The range in replicate particle collection efficiencies for the 6/7/82 series (where unsonicated 46-μm bead mixtures were used to seed the flow) overlapped only with the range of values for the 7/22/82 series. All particle collection efficiencies in series 8/24/82 (where 25-μm bead mixtures were sonicated before they were added to the bead tank) were about twice the values of the collection efficiencies during the other series. The variables between series (water temperature, flow speed, particle concentration, and bead mixture) which may have caused these differences in particle collection efficiencies are discussed below.

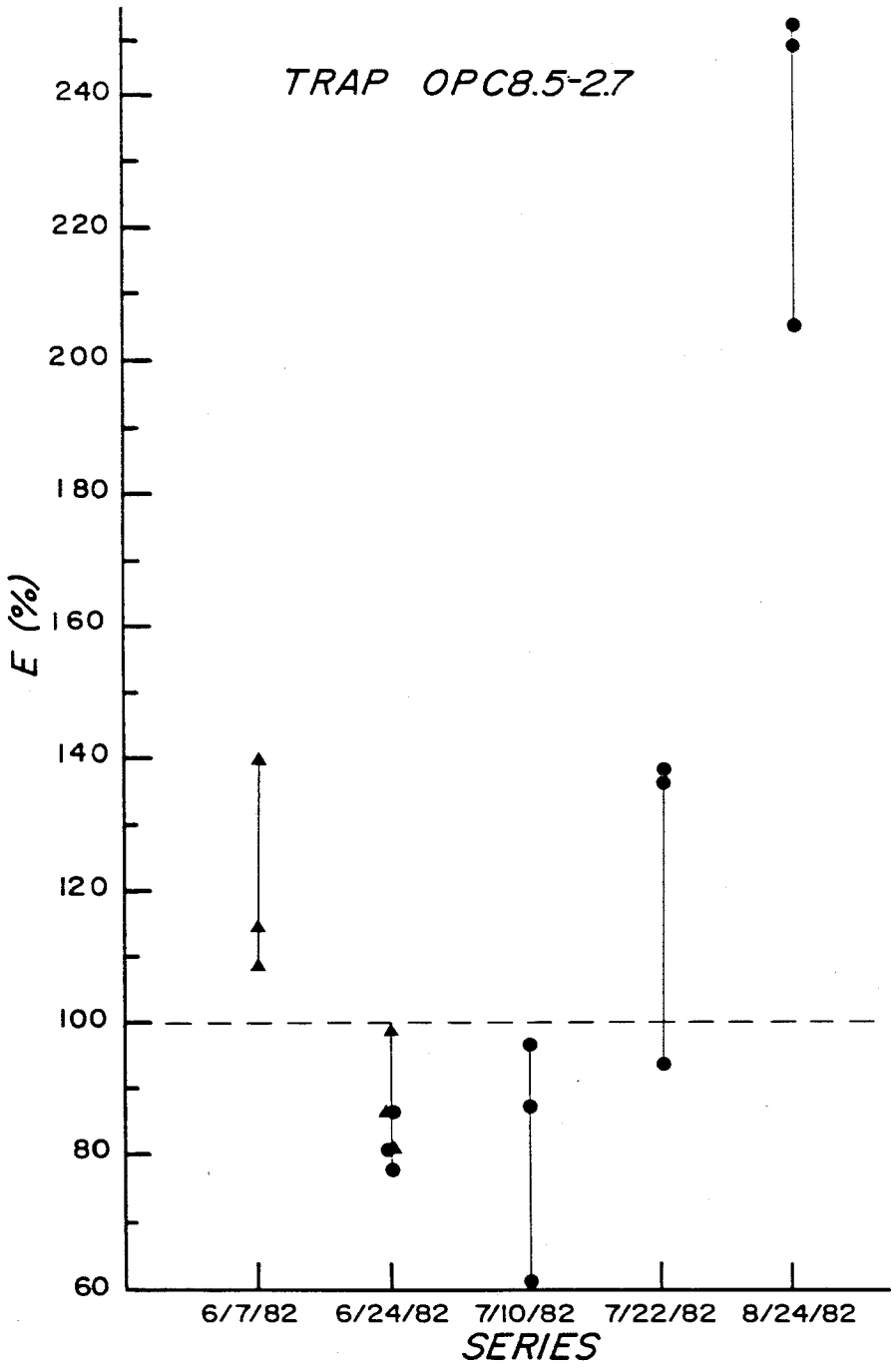


Figure 3.22: Particle collection efficiencies of trap OPC8.5-2.7, tested in all five series. Solid triangles are for traps positioned 34-cm above the flume bottom and solid circles are for traps positioned 47- or 51-cm above the bottom (see Table 3.10).

Water temperature differences between series and between replicate collections within a series already were accounted for in calculations of particle collection efficiencies; values of W_c were corrected for the specific water temperature (to 0.1°C) that occurred during each trap collecting interval (see Appendix III). However, variability in water temperature (and, thus, in ν) and in flow speed also would affect values of R_t, the trap Reynolds number, during each collecting interval. Because trap collection efficiency may be a function of R_t (see Section 3.1.2, criteria A), the correlation between these variables (plotted in Figure 3.23) was tested using the Spearman rank correlation coefficient. The H_o that there is no relationship between these two variables could not be rejected at $\alpha \leq 0.05$ ($r_s = 0.286$, $N = 18$). A range in R_t from 0.89×10^4 to 1.17×10^4, for all the replicates of trap OPC8.5-2.7 tested here, evidently does not constitute a significant dynamic range in conditions during trap collections.

Particle concentration in the flume varied from 4.5 to 15.5 mg/l among all the series (see Table 3.10); a significant negative correlation (at $\alpha \leq 0.01$ for $r_s = -0.701$, $N = 18$) between particle concentration and particle collection efficiency was detected for all replicates of trap OPC8.5-2.7, collecting for 8.5-min intervals. A close examination of the plotted values (Figure 3.24) indicates that this negative correlation may serve a predictive function for only four of the series. The efficiencies during the fifth series, 8/24/82, clump as anamolously high values at the midpoint of the range in C_i. For the rest of the data the relatively high

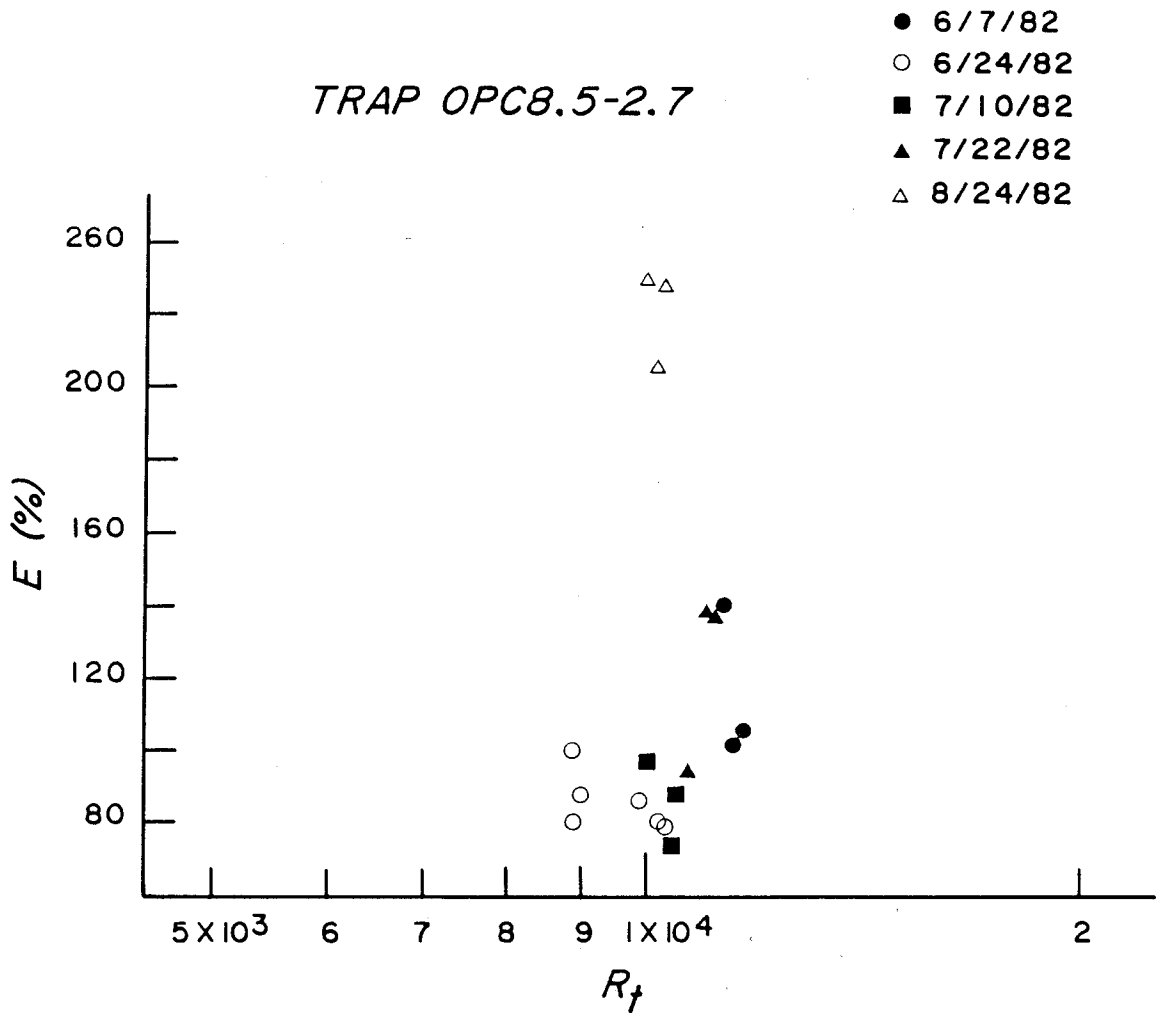


Figure 3.23: Relationship between particle collection efficiency and trap Reynolds number for all replicates of trap OPC8.5-2.7 tested for 8.5-min collecting intervals. Raw data are listed in Appendix III.

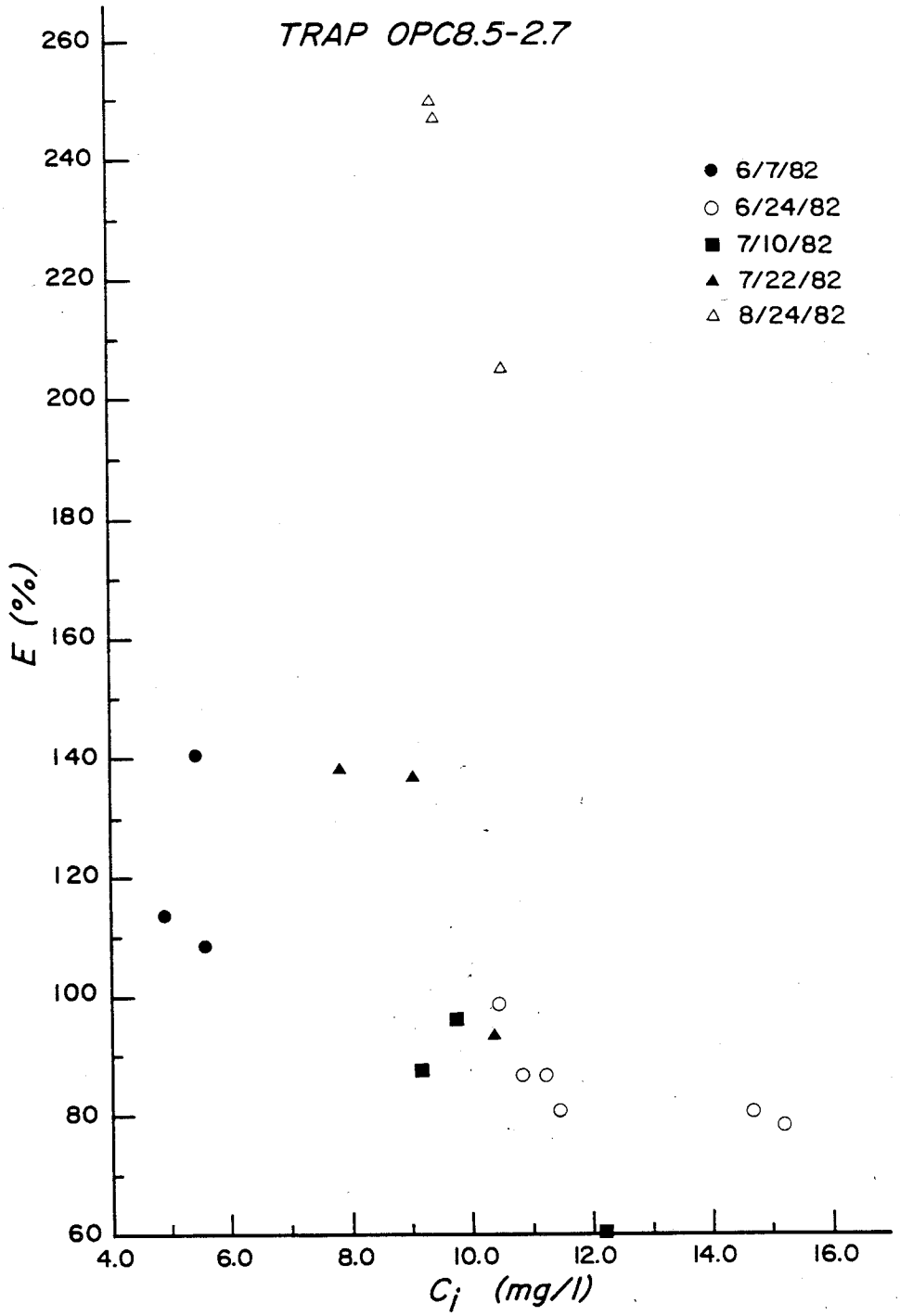


Figure 3.24: Relationship between particle collection efficiency and particle concentration in the seeded flume flow for all replicates of trap OPC8.5-2.7 tested for 8.5-min collecting intervals. Raw data are listed in Appendix III.

collection efficiencies for all three replicates during series 6/7/82 and for two replicates during series 6/24/82 (see also Figure 3.22) are associated with relatively low particle concentrations. A proposed mechanism linking the relative values of C_i and E to the values of W_c in the series is presented later (Section 3.4.4).

The effect on particle collection efficiency of variability between series in the bead mixtures used to seed the flow is difficult to assess because direct measurements were never made of the particle size distributions in water samples from the flume or from the traps. In theory, there were only two particle size distributions used in the series, the 46-μm bead mixture in the 6/7/82 series and the 25-μm bead mixture in the 6/24/82 series. However, efficiencies varied even for the three series using unsonicated 25-μm bead mixtures (series 6/24/82, 7/10/82 and 7/22/82) and there was a two-fold increase in efficiencies when sonicated 25-μm bead mixtures were used in series 8/24/82. These results suggest that (1) the frequency distributions of bead sizes in the flume and/or in traps differed between series, and/or (2) beads were not always falling as single particles, with the mean values of W_c calculated for each trap collecting interval. A hypothesis relating the between-series variability in particle collection efficiencies to possible differences in mean W_c between series is presented in Section 3.4.4.

3.3.6 Effect of trap design on particle collection efficiency

The raw data that were used to calculate relative particle collection efficiencies of all traps tested in this study are

presented in Appendix III and conditions in the flume during the series are listed in Table 3.10. For reference, the variability in the values of E_r for the three replicates of trap OPC8.5-2.7 tested during each series is shown in Figure 3.25. Precent CV for the mean E_r value of 100 percent for this trap design varied from 5.3 to 22.6 (mean = 14.7, SD = 7.1) among the five series.

Based on the relative differences in E_r values among all trap designs tested and on considerations of larval biology (discussed in Section 4.1.1), four "groups" of traps (labeled as "Group A" through "Group D" in the results presented below) were selected for deployment in the field. Results only for trap designs in these groups are presented here. Results for all other trap designs tested in this study are presented in Appendix II.

Group A consisted of the two trap designs (drawn to scale in Figure 3.26) tested most frequently in this study. Trap OPC8.5-2.7, a straight-sided cylinder, and trap OPG8.3-3.0, a small-mouth wide-body mouth jar. The traps were similar in height and mouth diameter. In all flume tests of this pair of trap designs, trap OPG8.3-3.0 collected approximately twice as many beads (by weight) as trap OPC8.5-2.7 (Figure 3.27). Mean E_r values for trap OPG8.3-3.0 were greater than mean E_r values of trap OPC8.5-2.7 by a factor of 2.1 in series 7/10/82, by a factor of 1.9 in series 7/22/82, by a factor of 2.3 for unscreened traps in series 8/24/82, and by a factor of 2.0 for screened traps in series 8/24/82.

In an attempt to assess whether or not the geometry of the trap near the trap mouth determines particle collection efficiency, a new

TABLE 3.10

Conditions and Traps Tested During Each Series of Flume Experiments

Date of Series	Traps tested (listed by code[1])	C_{bp} mean ± SD ( ) = N (mg/l)	Height[2] of all trap mouths above bottom (cm)	Conditions During Trap Tests: Time interval when traps were tested (EST[3]) ( ) = total no. hrs.	Approx. temp. (°C) range during all trap tests ( ) = mean rate of change in °C/hr	Range of flume water height (cm)	Measured flow speed[4] mean ± SD ( ) = N (cm/sec)	Bead mixture[5] used to seed flow	Approx. range in C_i[6] (mg/l)
5/25/82-5/26/82	no traps tested: methods, volume, and speed comp.	not applicable	water samples taken 34-cm above bottom	comparisons made from 1128-1408 (2.7)	29.6-30.8 (0.3)	51.5-52.0	none	46μm	3.5-5.5[7]
6/07/82[8]	OPC8.5-1.0 OPC8.5-1.9 OPF8.5-1.9 OPC8.5-2.7	1.00 ± 0.38 (22)	34	1410-1946 (5.6)	20.5-22.3 (0.3)	58.5-61.0	none	46μm	4.5-8.5
6/24/82[9]	OPC8.5-2.7 OPC8.5-3.6 speed comparison	0.51 ± 0.44 (22)	34, 47[10]	1322-1922 (6.0)	22.0-24.4 (0.4)	68.5-71.0	11.0 ± 0.8 (98) 11.0 ± 0.9 (25) 11.1 ± 0.7 (52) 10.6 ± 0.8 (40)	25μm	9.0-15.5
7/10/82	TBC1.7-3.0 TBC3.6-3.1 TBC7.4-2.9 OPC8.5-2.7 OPC8.5-2.7S[11] OPG8.3-3.0 OPF8.3-1.9	1.39 ± 0.68 (22)	47	1304-1756 (4.9)	23.9-25.8 (0.5)	69.5-71.5	none	25μm	8.5-13.0
7/22/82	TBC1.7-3.0 TBC3.6-3.1 TBC7.4-2.9 OPC8.5-2.7 OPG8.5-3.0 OPF14.1-1.6	1.32 ± 1.01 (22)	51	0823-1320 (5.0)	25.9-27.7 (0.4)	69.5-73.5	10.1 ± 0.7 (55) 10.3 ± 0.6 (61)	25μm	7.5-11.0

TABLE 3.10 (cont. - 2)

Date of Series	Traps tested (listed by code[1])	C_{bp} mean ± SD () = N (mg/l)	Height[2] of all trap mouths above bottom (cm)	Conditions During Trap Tests: Time interval when traps were tested (EST[3]) ( ) = total no. hrs.	Approx. temp. (°C) range during all trap tests ( ) = mean rate of change in °C/hr	Range of flume water height (cm)	Measured flow speed[4] mean ± SD ( ) = N (cm/sec)	Bead mixture[5] used to seed flow	Approx. range in C_i[6] (mg/l)
8/24/82	TBC14.7-1.6 TBF14.7-1.6S TBC14.7-2.9 OPC8.5-1.0TB[12] OPC8.5-1.9TB OPC8.5-2.7TB OPC8.5-2.7BB[13] OPC8.5-2.7S OPC8.5-2.7 OPC8.5-3.6 OPP8.3-2.7 OPG8.5-3.0 OPG8.5-3.0S OPGC8.5-3.6	1.44 ± 0.33 (22)	51	1152-1940 (7.8)	24.9-27.3 (0.3)	69.0-75.0	none	25μm	8.5-11.5

1. Trap dimensions and codes are given in Table 3.1.
2. Heights are given to ± 0.5 cm.
3. Eastern Standard Time.
4. These measurements were taken over various time intervals while traps were collecting particles; see Section 3.2.4 for description of how measurements were taken.
5. Characteristics of these bead mixtures are described in Section 3.2.5.
6. In each series, less than 10 percent of the measured bead concentrations were outside this range.
7. These concentrations include C_{bp}.
8. All traps were tested for 4.5-, 6.5-, and 8.5-min intervals.
9. All traps were tested for 4.5-, 6.5-, 8.5- and 16.5-min intervals.
10. Three additional replicates of trap OPC8.5-2.7 were tested at this height for 8.5-min intervals; all other traps were tested at 34-cm (see Appendix III).
11. S = screened; a fine filament ($\leq$ 0.25 mm in diameter) plastic screen having 16-mm^2 openings was secured tightly over the trap mouth during collections.
12. TB = top baffled; a "honeycomb" baffle 78-mm tall with cells ~ 10 mm in diameter was cut to exactly fill the inside diameter of the trap and was placed inside the trap, flush with the trap mouth.
13. BB = bottom baffled; a honeycomb baffle (described in footnote 12) was pushed down inside the trap to sit directly on the trap bottom.

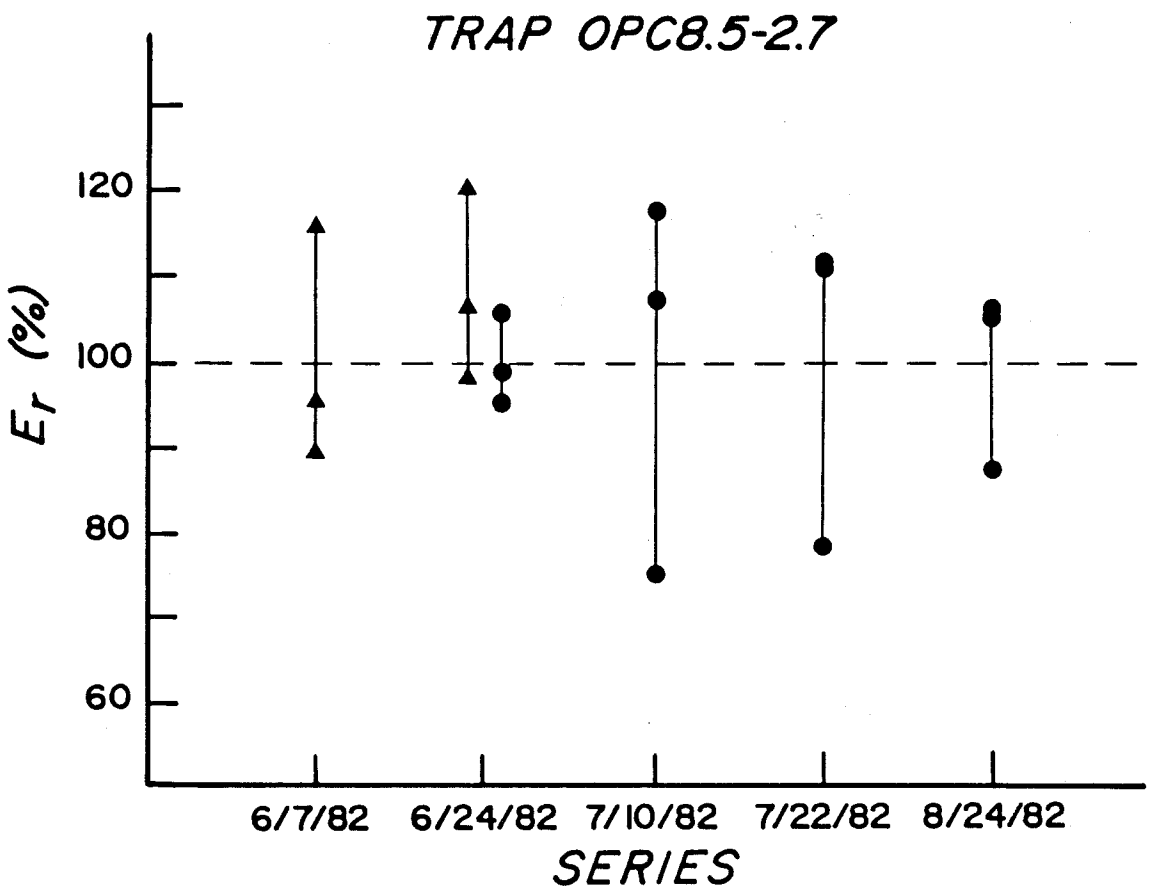


Figure 3.25: Relative particle collection efficiencies of trap OPC8.5-2.7, tested during all of the series. By definition, the mean value of E_r for this trap design is 100 percent. Traps positioned 34-cm above the bottom are indicated by solid triangles and traps positioned 47- or 51-cm above the bottom are indicated by solid circles. For the 6/24/82 series, the mean collection efficiency only for the three traps placed 47-cm above the bottom was used as E_s in calculations of E_r for all other traps tested in this series. For comparison, the E_r values for the three replicates placed 34-cm above the bottom during this series, are also plotted here. Raw data for the E_r calculations are listed in Appendix III.

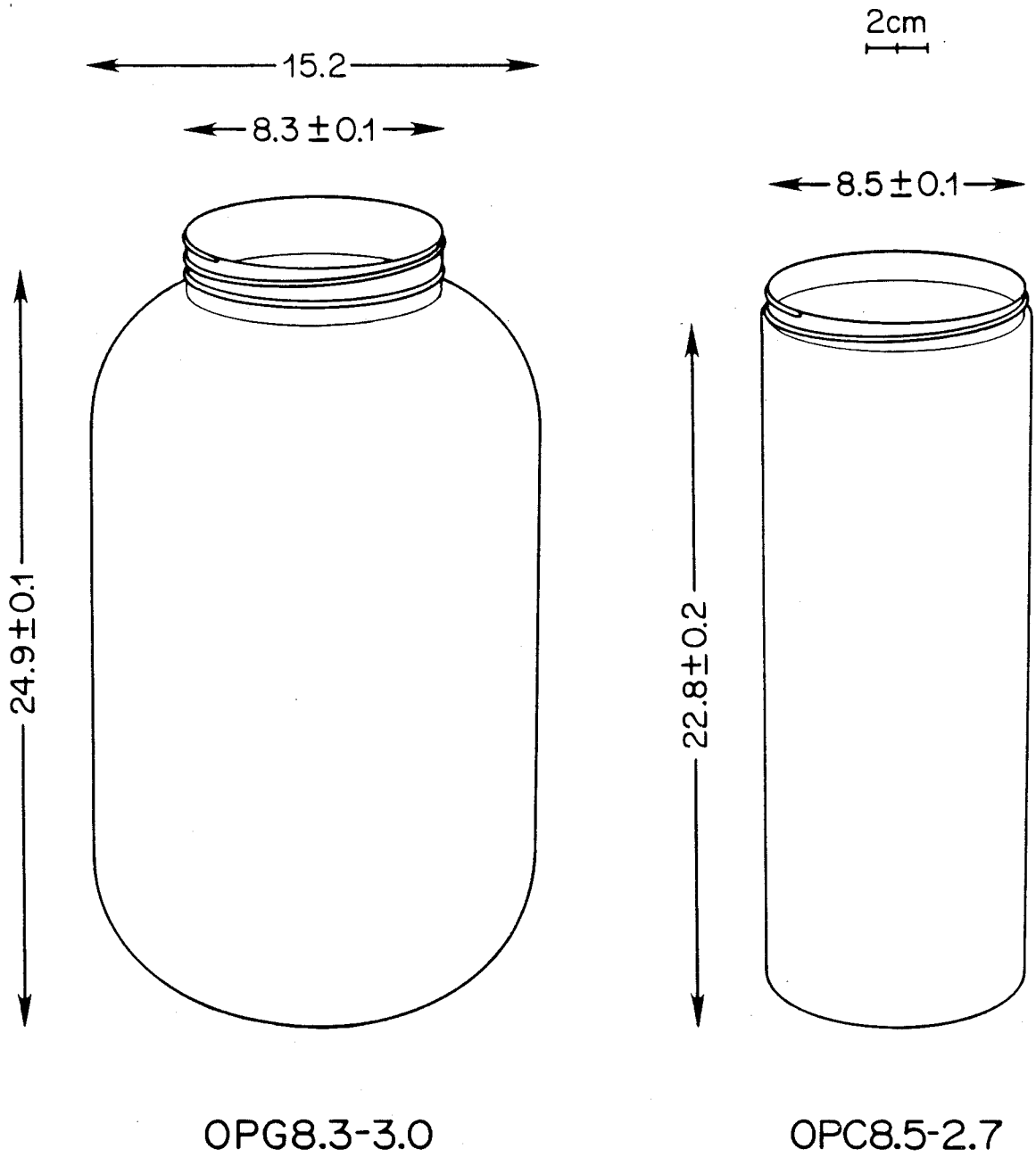


Figure 3.26: Diagrams, to scale, of the Group A traps, OPG8.3-3.0 and OPC8.5-2.7. Dimensions are indicated, on the Figure, of the inside mouth diameter and total height of both traps, and of the maximum outside diameter of trap OPG8.3-3.0; other dimensions are listed in Table 3.1.

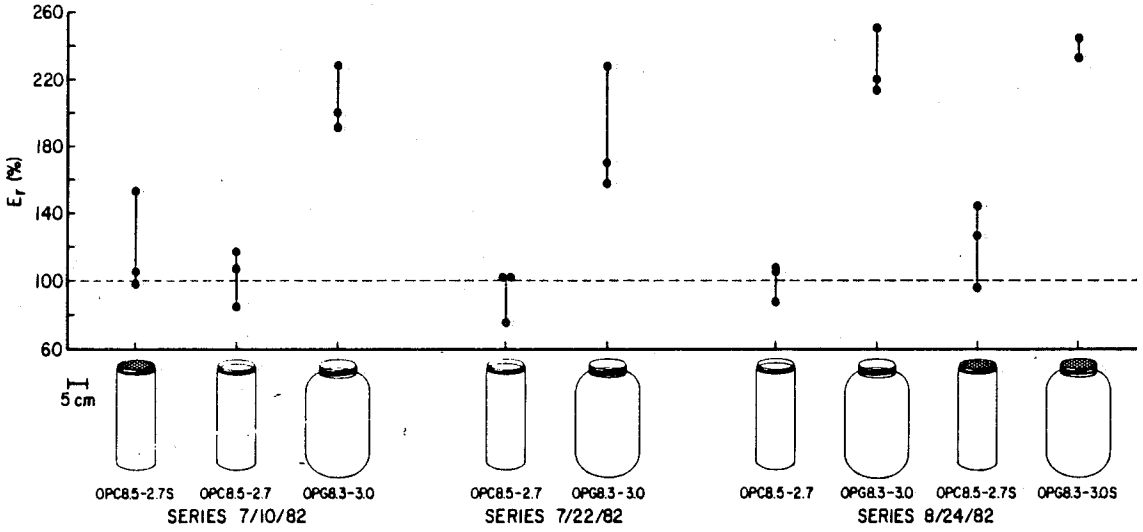


Figure 3.27: Relative particle collection efficiencies of the Group A traps, OPG8.3-3.0 and OPC8.5-2.7, tested during series 7/10/82, 7/22/82 and 8/24/82. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

trap design (OPGC8.5-3.6) was made by gluing a cylinder (trap OPC8.5-1.0) on top of trap OPG8.3-3.0. Thus, a cylindrical trap geometry was reconstructed near the trap mouth. The a priori hypothesis was that relative particle collection efficiencies of this new trap (OPGC8.5-3.6) should be similar to the efficiencies of a straight-sided cylinder of similar height and mouth diameter, trap OPC8.5-3.6. This H_0 was rejected at $\alpha \leq 0.05$ (Mann-Whitney U test) in tests of these two trap designs during series 8/24/82 (Figure 3.28). In fact, values of E_r for trap OPGC8.5-3.6 encompassed the range in values for trap OPG8.3-3.0, tested during this series. Other mechanisms that would account for the relative overcollection of particles by the small-mouth wide-body traps compared to the straight-sided cylinders, are discussed later (Section 3.4.5).

Group B consisted of the two traps in Group A (traps OPG8.3-3.0 and OPC8.5-2.7) and a cylindrical trap with a Plexiglas circular plate (6-mm thick) glued flush with the trap mouth (trap OPP8.3-2.7, diagramed in Figure 3.29). During series 8/24/82, the latter trap design relatively undercollected particles compared to collections by both the traps in Group A (Figure 3.30). Mean E_r values of traps OPG8.3-3.0 and OPC8.5-2.7 were greater than the mean E_r values of trap OPP8.3-2.7 by factors of 5.2 and 2.3, respectively. Collections by trap OPP8.3-2.7 were observed directly, by the author, during the flume experiments. The leading edge of the plate was scoured by the flow to a distance of ~ 2 cm toward the center of the plate; particles were observed accumulating on the plate surface beyond this

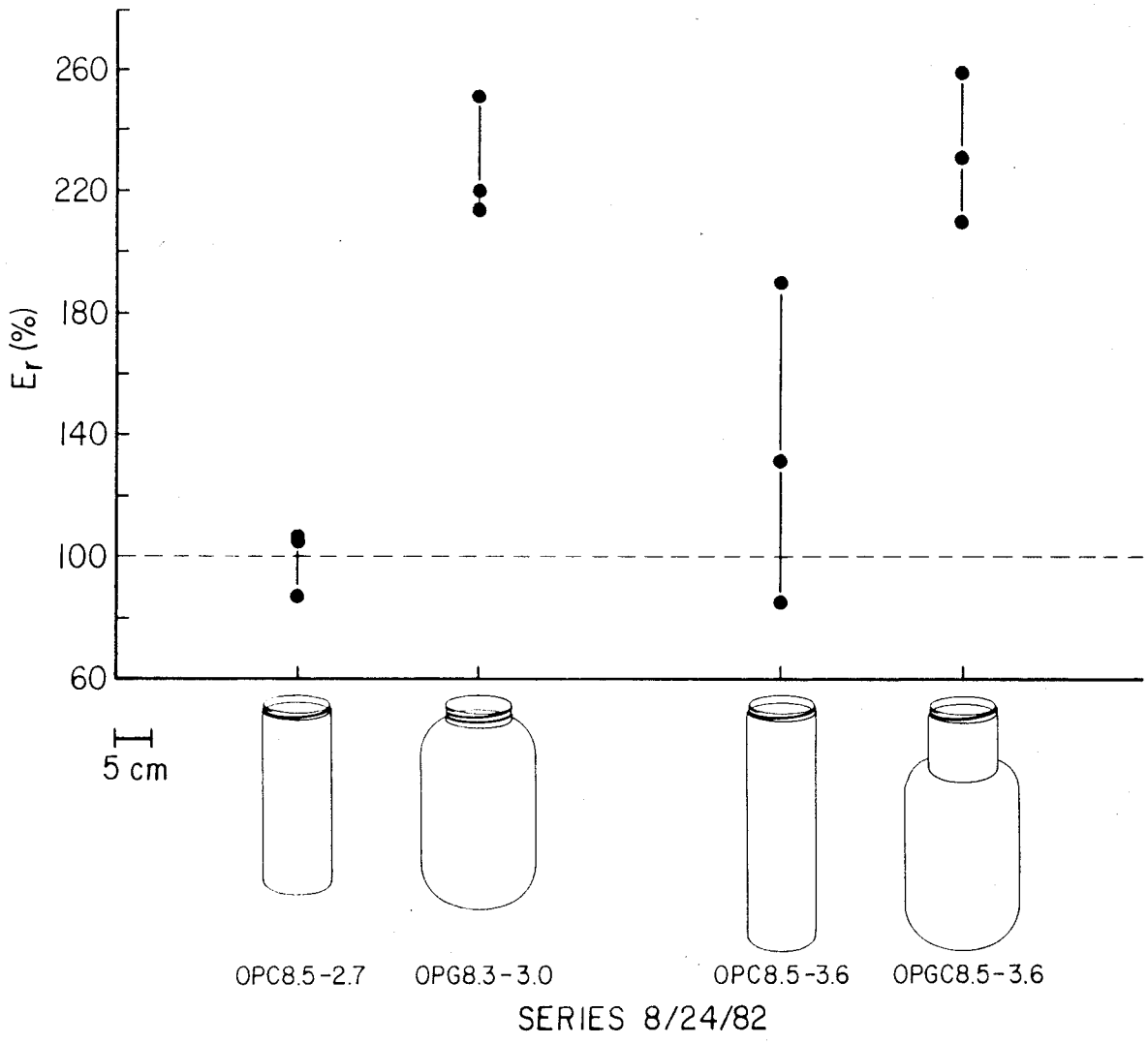


Figure 3.28: Relative particle collection efficiencies of traps OPG8.3-3.0, OPC8.5-2.7, OPGC8.5-3.6, and OPC8.5-3.6 tested during series 8/24/82. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

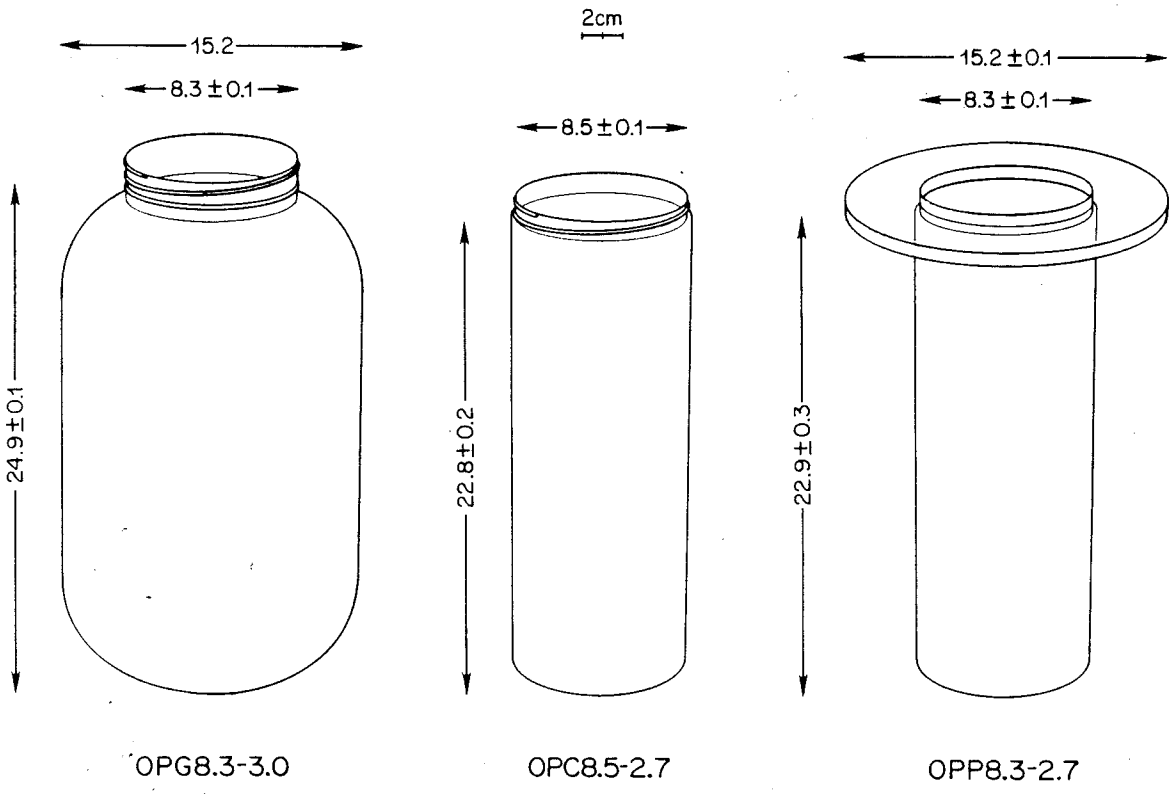


Figure 3.29: Diagrams, to scale, of the Group B traps, OPG8.3-3.0, OPC8.5-2.7, and OPP8.3-2.7. Dimensions are indicated, on the Figure, of the inside mouth diameter and total height of all three traps and of the maximum outside diameter of traps OPG8.3-3.0 and OPP8.3-2.7; other dimensions are listed in Table 3.1.

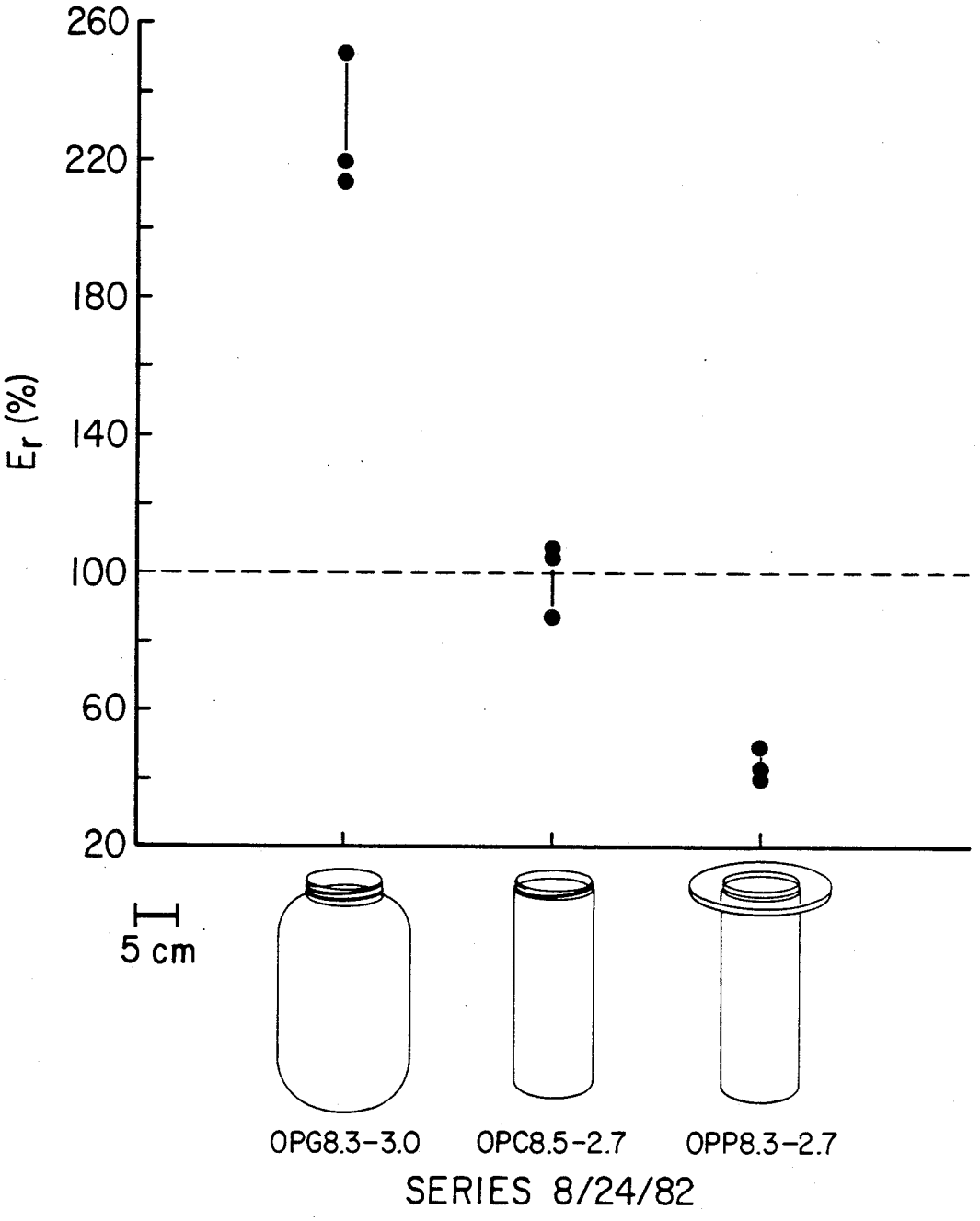


Figure 3.30: Relative particle collection efficiencies of the Group B traps, OPG8.3-3.0, OPC8.5-2.7 and OPP8.3-2.7, tested during series 8/24/82. Raw data for calculated E_r values are given in Appendix III. Traps are drawn, to scale, below the Figure.

scoured region. The significance of these observations to the relative undercollection characteristics of this trap design are discussed later (Section 3.4.5).

Group C consisted of three traps, all straight-sided cylinders with the same mouth diameter (see diagrams in Figure 3.31). One trap (OPC8.5-1.0) had an aspect ratio of 1.0; the other two traps had aspect ratios of 1.9, but one trap (OPF8.5-1.9) contained a funnel (inside diameter at bottom of funnel = 1.1 ± 0.1 cm) that was flush with the trap mouth and the other trap did not. Collections by traps OPC8.5-1.0 and OPC8.5-1.9 during series 6/7/82 were similar (mean E_r = 72.9 ± 8.7 percent for trap OPC8.5-1.0 and mean E_r = 80.0 ± 7.0 percent for trap OPC8.5-1.9, Figure 3.32), but both traps were relative undercollectors (by ~ 75 percent) compared to collections by trap OPC8.5-2.7 during this series (see Figure 3.25). During series 6/7/82, trap OPF8.5-1.9 undercollected particles relative to traps OPC8.5-1.0 and OPC8.5-1.9 (Figure 3.32). The mean E_r of trap OPF8.5-1.9 was exceeded by a factor of 3.3 for trap OPC8.5-1.0, by a factor of 3.6 for trap OPC8.5-1.9, and by a factor of 4.6 for trap OPC8.5-2.7. When trap OPF8.5-1.9 was uncapped in the flume, air was trapped between the top of the funnel and the side of the cylinder; shaking the trap while it was in place allowed some of this air to escape. Also, during processing of samples from trap OPF8.5-1.9, any particles on the funnel were not included as part of the trap sample (i.e., the funnel was not "washed").

To determine the proportion of beads that enter the trap mouth, but do not pass through the bottom of the funnel during 8.5-min

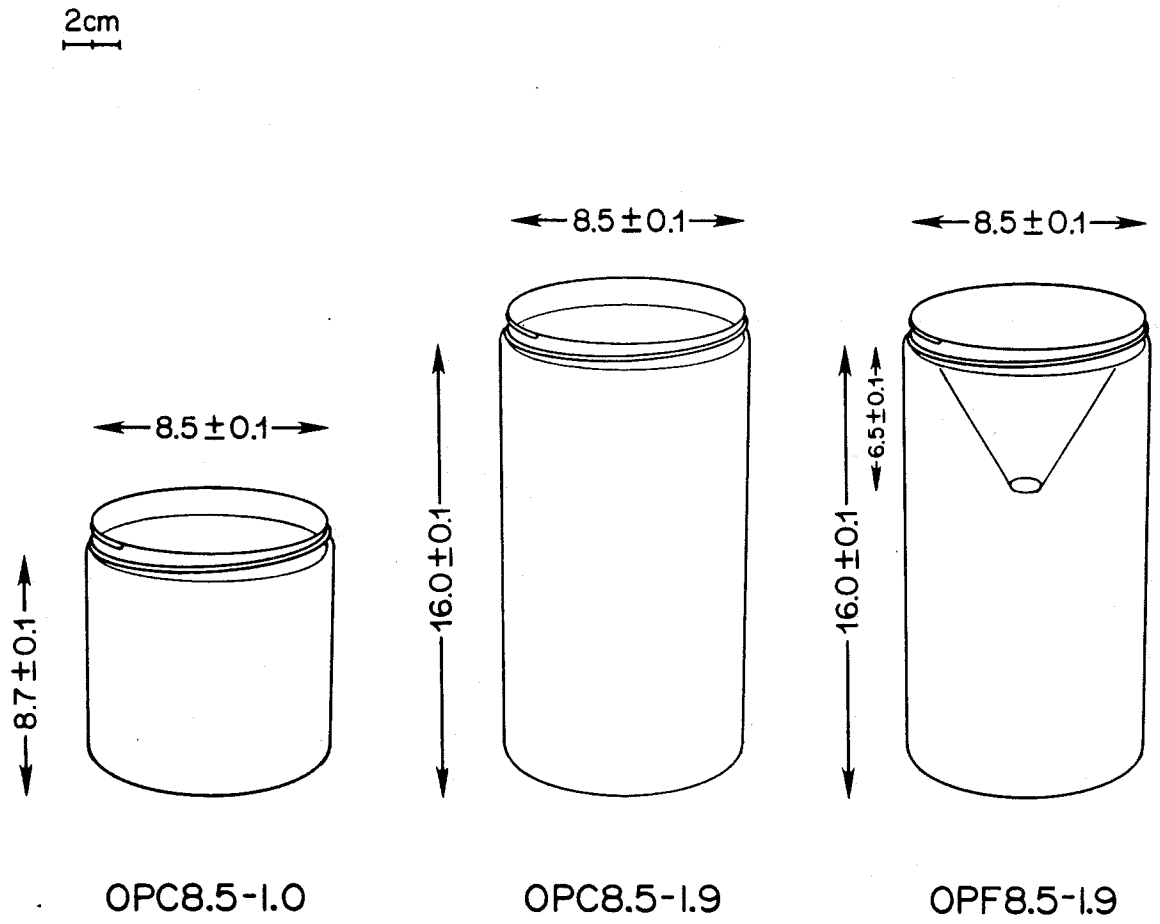


Figure 3.31: Diagrams, to scale, of the Group C traps, OPC8.5-1.0, OPC8.5-1.9, and OPF8.5-1.9. Dimensions are indicated, on the Figure, of the inside mouth diameter and total height of all three traps, and of the total height of the funnel inside trap OPF8.5-1.9; other dimensions are listed in Table 3.1.

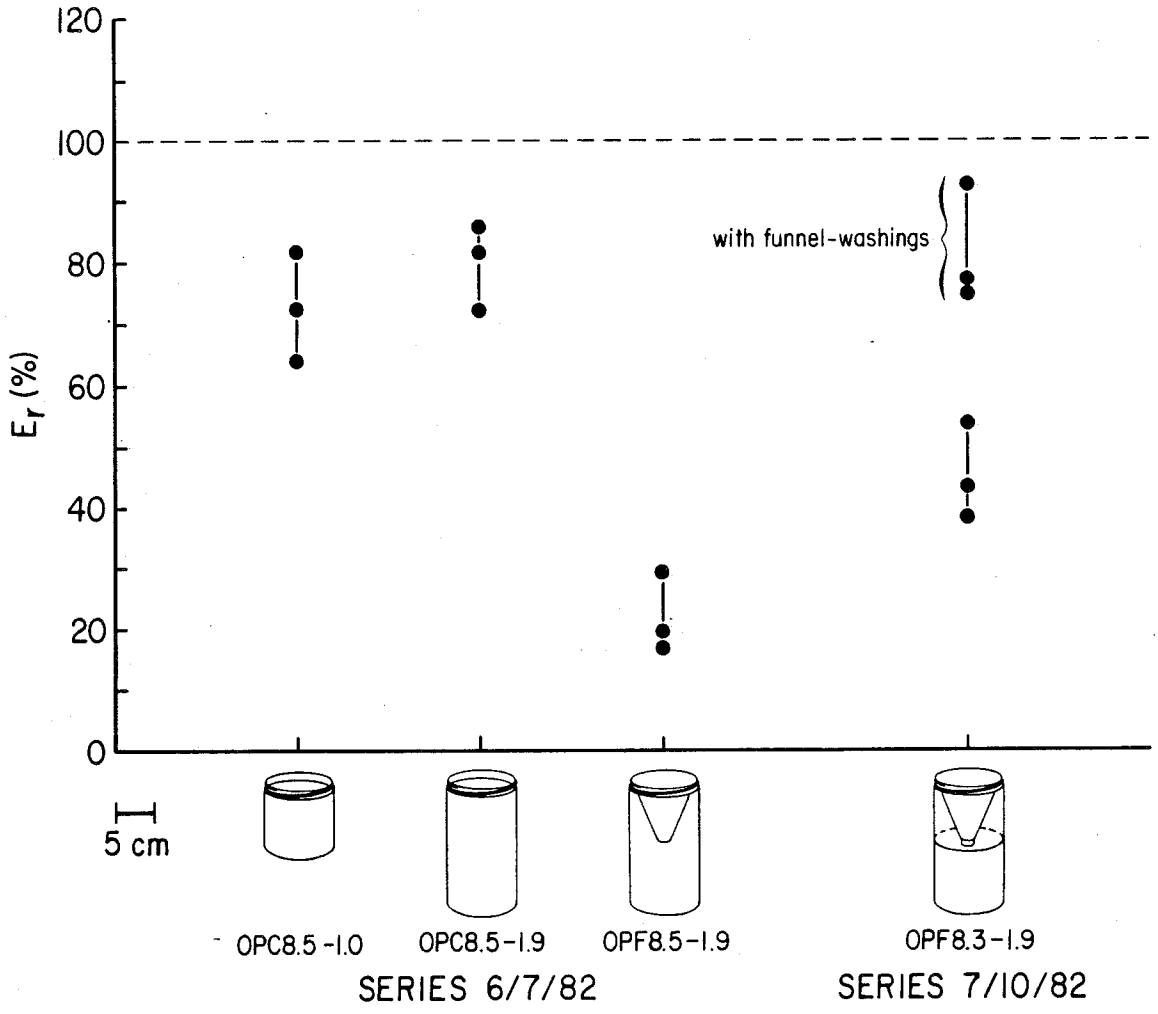


Figure 3.32: Relative particle collection efficiencies of the Group C traps, OPC8.5-1.0, OPC8.5-1.9 and OPF8.5-1.9, during 8.5-min collecting intervals in series 6/7/82 and of trap OPF8.3-1.9 during series 7/10/82. The E_r values for traps OPF8.5-1.9 and OPF8.3-1.9 do not include the washings from the funnels except where noted on the figure. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

collections, a new funnel-trap design (trap OPF8.3-1.9) was tested during series 7/10/82. This trap was a cylinder with similar outside dimensions to trap OPF8.5-1.9 (see Table 3.1), but the trap was constructed in two parts. The top part of the trap was a cylinder (trap OPC8.5-1.0) containing a funnel (8.4 ± 0.1 cm in height, with an inside diameter at the bottom of the funnel of 1.1 ± 0.1 cm) that protruded through the solid bottom of the cylinder. The bottom part of the trap was another cylinder (trap OPC8.5-1.0); the two parts were taped together during collections. The sides of the top cylinder were perforated so that water surrounded the outside of the funnel but could not enter the bottom cylinder; this was necessary so the trap would not float. At the end of a trap collecting interval, the top cylinder was removed and the inside of the funnel was washed with prefiltered (through a 0.45-μm Millipore filter) deionized water into a separate jar. The bottom cylinder was capped and the two samples were processed separately. Trap OPF8.3-1.0 was tested during series 7/10/82, but the two cylinders in Group C were not tested in this series.

Trap OPF8.3-1.0 significantly ($\alpha \leq 0.05$, Mann-Whitney U test) undercollected particles relative to trap OPC8.5-1.7 during series 7/10/82, only when the funnel-washings were not included as part of the sample (see Figures 3.32 and 3.25). The mean E_r of trap OPF8.3-1.0 was 42.0 ± 12.4 percent without funnel-washings and was 81.6 ± 9.9 percent (mean E_r for trap OPC8.5-2.7 was 99.9 ± 22.6 percent). Considerably more air was trapped inside this funnel trap design, compared to trap OPF8.5-1.9, and rigorous shaking

was required to dislodge the air.

Group D consisted of the cylinder (OPC8.5-2.7) in Group A and B, and two cylinders with larger mouth diameters but total heights similar to trap OPC8.5-2.7; one cylinder (TBF14.7-1.6) contained a funnel that protruded slightly above the trap mouth and the other cylinder (TBC14.7-1.6) did not (see diagrams in Figure 3.33). For tests of the Group D traps during series 8/24/82, trap TBF14.7-1.6 was screened and both screened and unscreened OPC8.5-2.7 traps were tested.

During series 8/24/82, relative particle collection efficiencies of the three Group D trap designs were not substantially different, although all E_r values for trap TBC14.7-1.6 did not overlap with E_r values for trap OPC8.5-2.7 (Figure 3.34). The variation in the three replicate collections by trap TBC14.7-1.6 was unusually low (CV = 1.9 percent for trap TBC14.7-1.6 compared to CV = 10.8 percent for trap OPC8.5-2.7 and CV = 14.6-15.1 percent for trap TBF14.7-1.6S during series 8/24/82). Because this extremely low variability is less than even the minimum measurement error of ~ 5 percent, calculated for trap tests in this flume study (see Section 3.4.3), collections by trap TBC14.7-1.6 are not considered to be statistically lower than collections by trap OPC8.5-2.7 during this series. With or without inclusion of the funnel-washings, the ranges in E_r values for trap TBF14.7-1.6S overlapped with E_r values for traps OPC8.5-2.7 and TBC14.7-1.6. However, the ranges in E_r values did not overlap for trap OPC8.5-2.7S and trap TBF14.7-1.6S when funnel-washings were not included in the samples.

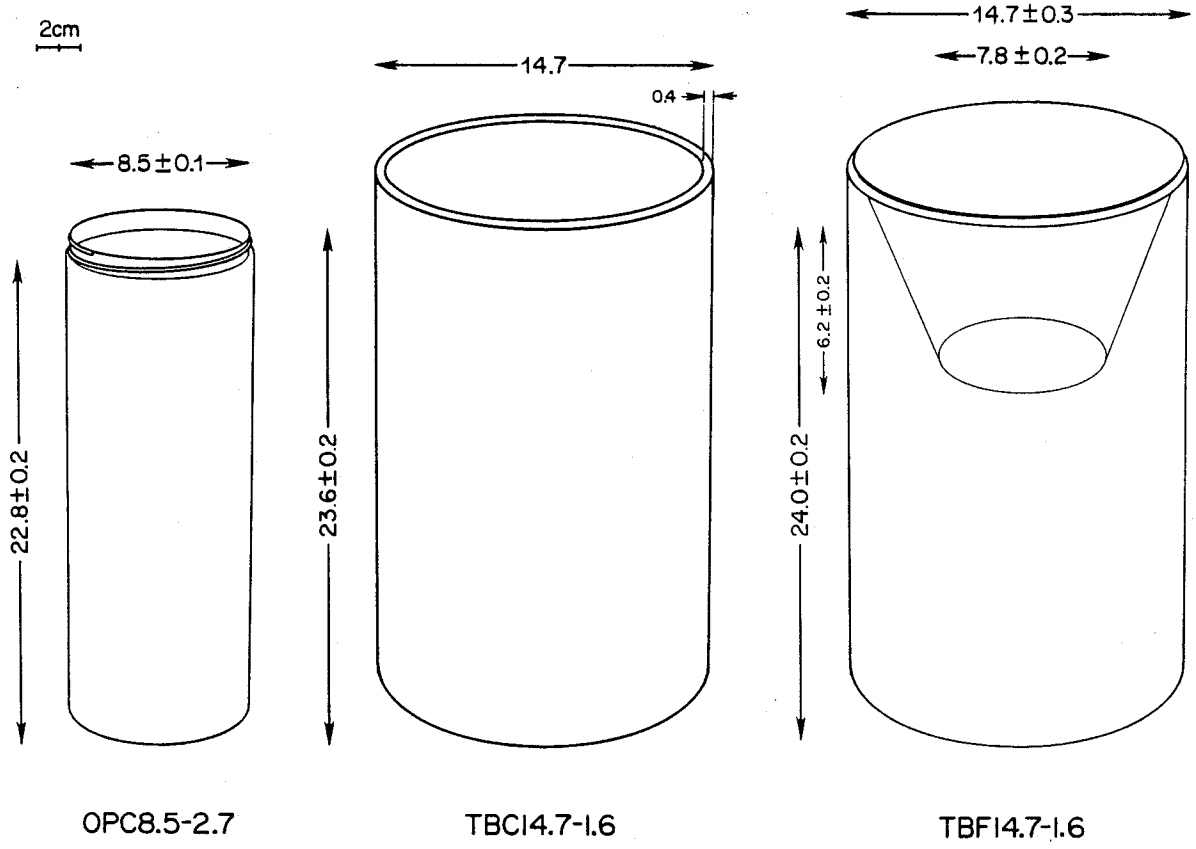


Figure 3.33: Diagrams, to scale, of the Group D traps, OPC8.5-2.7, TBC14.7-1.6, and TBF14.7-1.6. Dimensions are indicated, on the Figure, of the inside mouth diameter and total height of all three traps, of the wall thickness of traps TBC14.7-1.6 and TBF14.7-1.6, and of the height and inside diameter at the bottom of the funnel in trap TBF14.7-1.6; other trap dimensions are listed in Table 3.1.

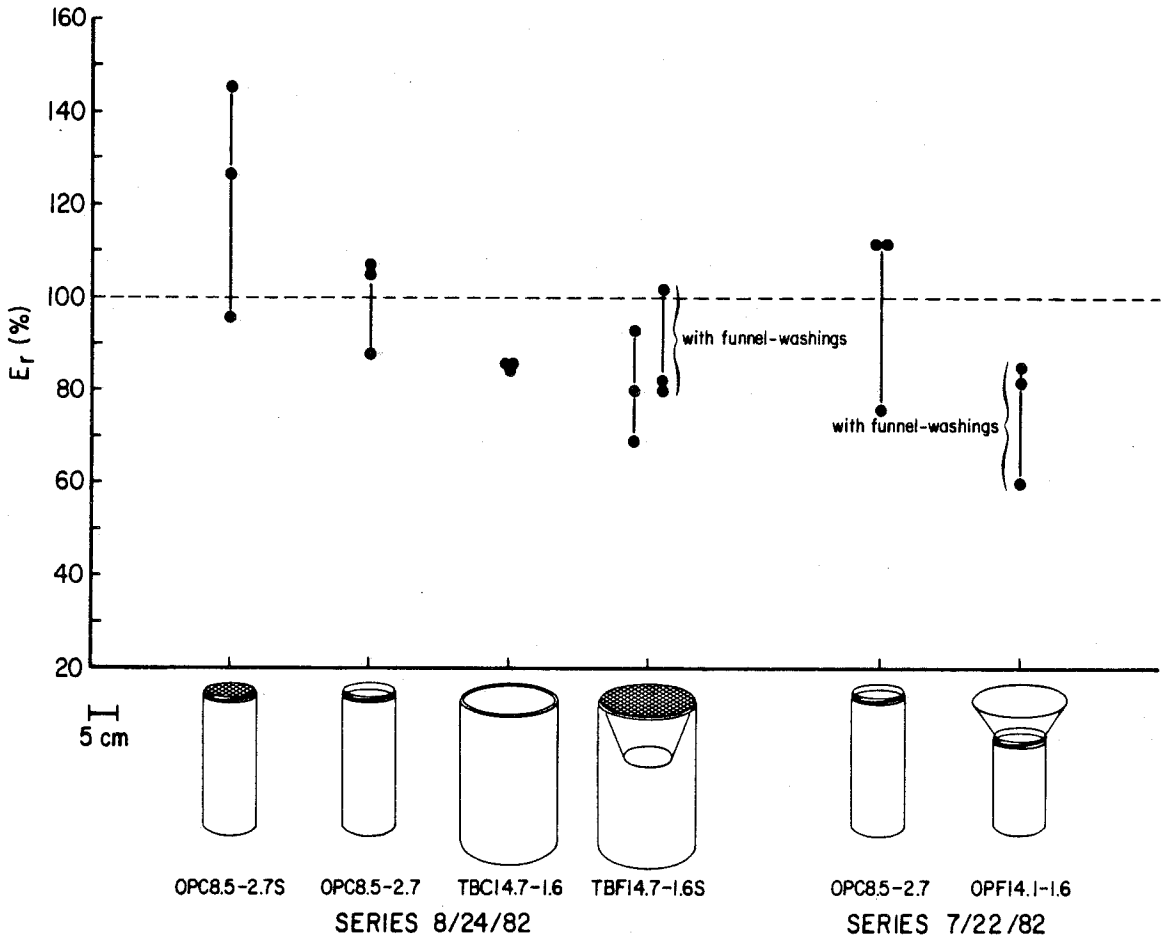


Figure 3.34: Relative particle collection efficiencies of the Group D traps, OPC8.5-2.7 (screened and unscreened), TBC14.7-1.6 and TBF14.7-1.6 (screened), during series 8/24/82 and of traps OPC8.5-2.7 and OPF14.1-1.6 during series 7/22/82. The E_r values for traps TBF14.7-1.6S and OPF14.1-1.6 do not include the washings from the funnels, except where noted in the Figure. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

Another large-diameter funnel-trap (trap OPF14.1-1.6) was tested in conjunction with trap OPC8.5-2.7, during series 7/22/82. This funnel-trap consisted of a cylinder (trap OPC8.5-1.9) with a large funnel (inside mouth diameter = 14.1 cm, height = 6.8 ± 0.1 cm) resting on top; the inside diameter at the bottom of the funnel was the same as the mouth diameter of the cylinder (8.5 ± 0.1 cm) and the total height of the trap was 22.8 ± 0.2 cm, as for trap OPC8.5-2.7. The funnel was taped onto the top of the cylinder during collections and the entire contents of the trap were processed (that is, the funnel-washings were included in the samples).

Collections by trap OPC8.5-2.7 and OPF14.1-1.6 overlapped in tests during series 7/22/82 (Figure 3.34); however, the mean E_r for trap OPC8.5-2.7 exceeded the mean E_r for trap OPF14.1-1.6 by a factor of 1.3. A hypothesis to explain the curious findings reported here, that some funnel traps relatively undercollect particles, while others do not, is presented in Section 3.4.5.

3.3.7 Visualization of flow patterns near the mouths of several trap designs

Visualization of flow patterns near the mouths of six trap designs tested in this study are presented in Figures 3.35 through 3.41. A general description of the observed flow patterns is given here. In Section 3.4.5, the qualitative flow observations are integrated with the quantitative particle collection efficiency data in a discussion of the nature of the trap biases demonstrated in this study.

The flow passing $\geq$ 3.1-cm above the cylindrical trap,

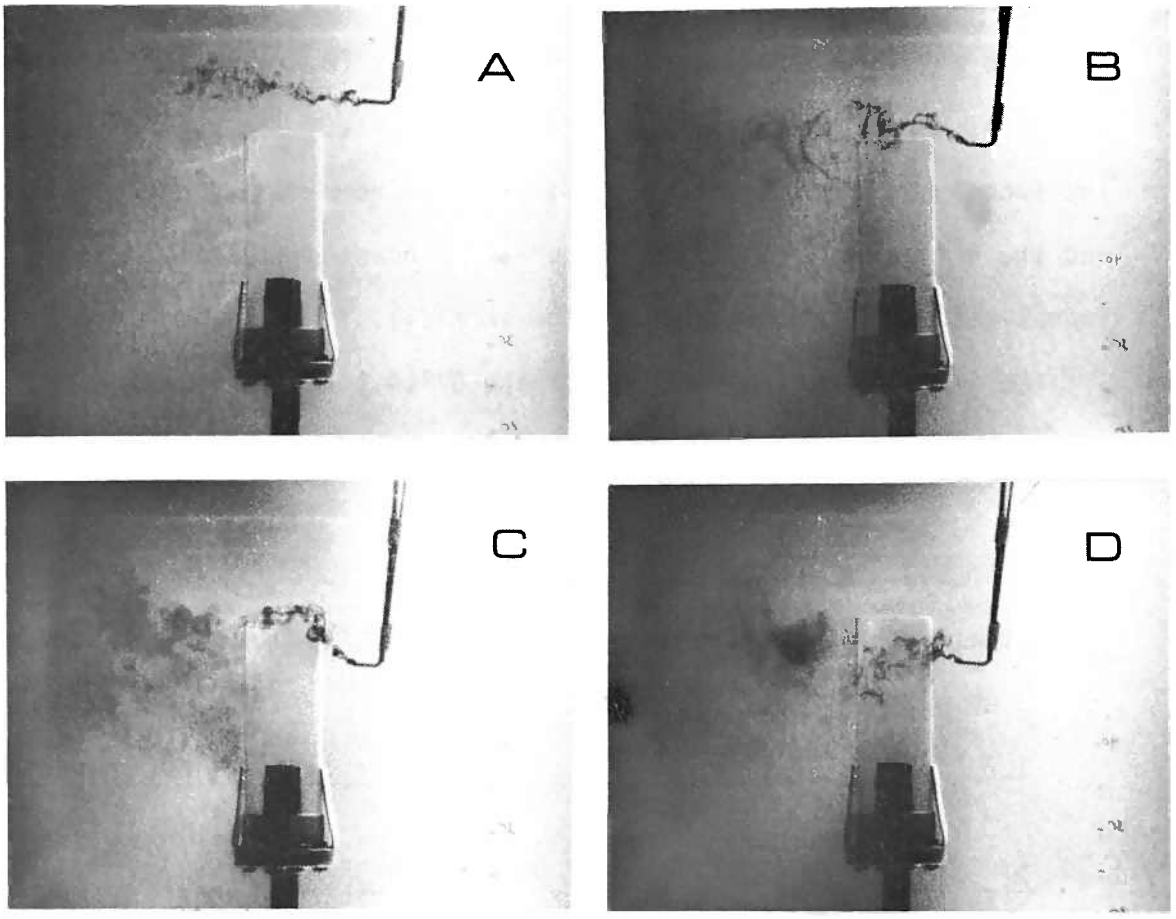


Figure 3.35: Visualization, using dye (see caption to Figure 3.17), of flow patterns near the mouth of trap TBC7.4-2.9. The flow is shown here moving from the right to the left of each frame. The probe was positioned about 3.1-cm above the trap mouth (A), and 1.0-cm (B), 4.2-cm (C), and 4.7-cm (D) below the trap mouth.

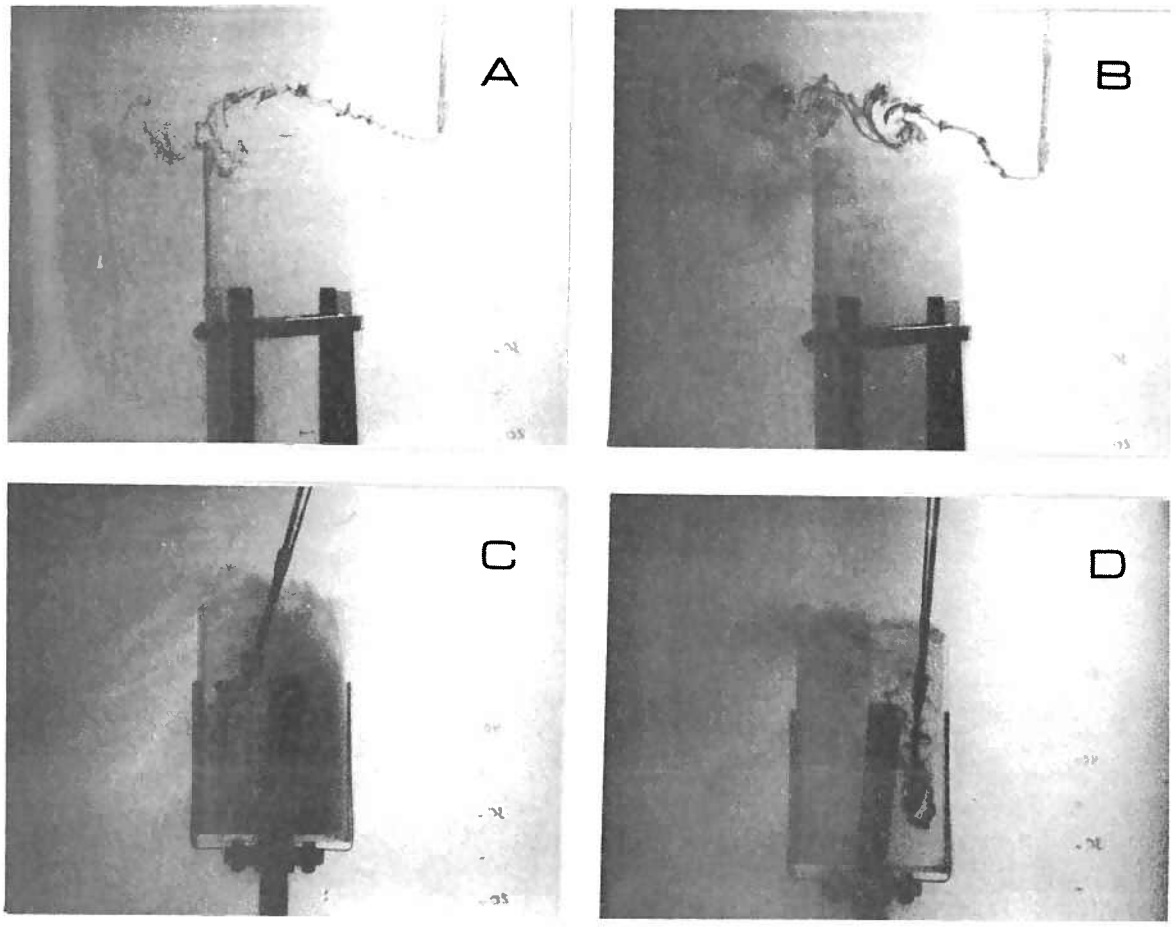


Figure 3.36: Visualization, using dye (see caption to Figure 3.17), of flow patterns near the mouth of trap TBC14.7-2.9 and inside trap TBC14.7-1.6. The flow is shown here moving from the right to the left of each frame. Trap TBC14.7-2.9 is shown in pictures A and B, and trap TBC14.7-1.6 in pictures C and D. The probe was positioned about even with the trap mouth (A), and 3.2-cm (B), 9.1-cm (C), and 19.3-cm (D) below the trap mouth.

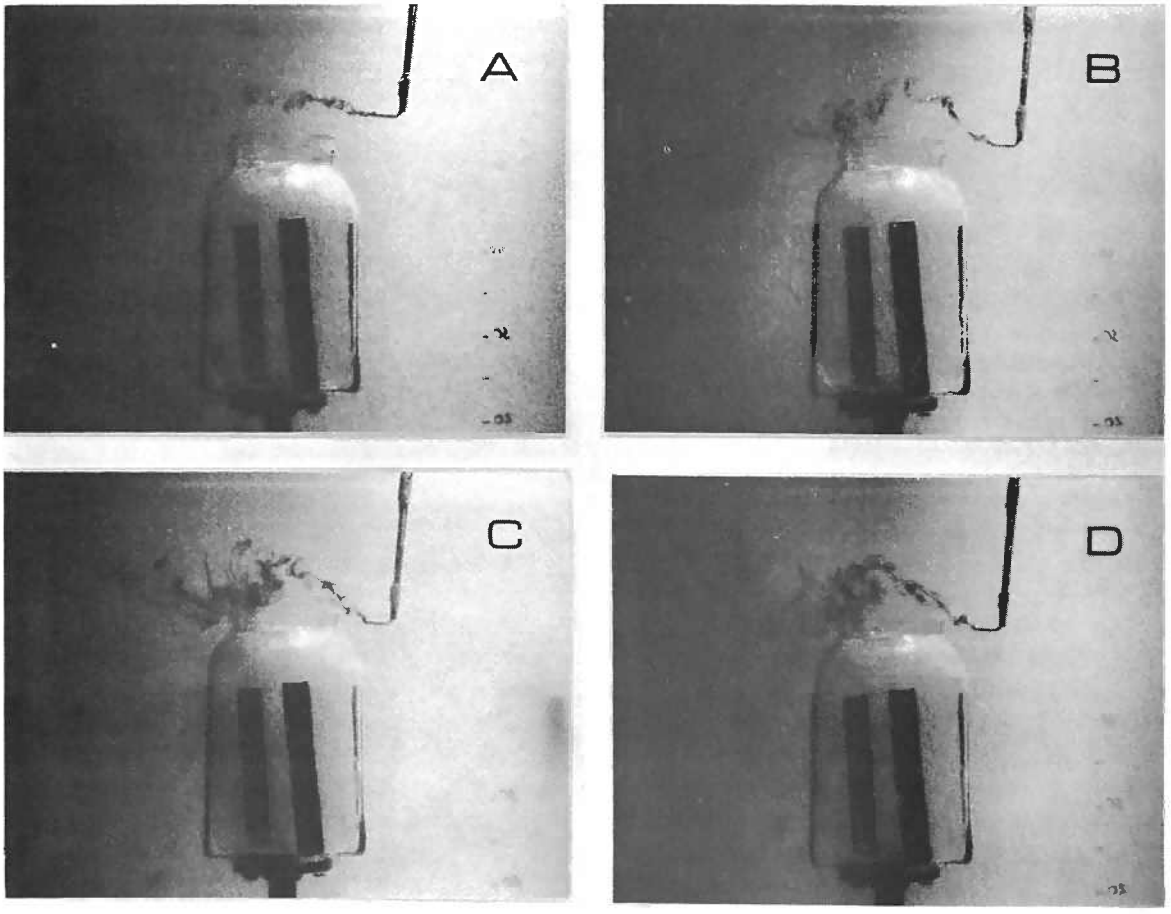


Figure 3.37: Visualization, using dye (see caption to Figure 3.17), of flow patterns near the mouth of a trap that was similar in design to trap OPG8.3-3.0. The trap pictured here was 24.9-cm tall, 9.7 cm in inside mouth diameter, 10.5 cm in outside diameter at the trap mouth, and 15.0 cm in maximum body diameter; the smaller diameter of the trap extended to a distance of 3.1-cm below the trap mouth. The flow is shown here moving from the right to the left of each frame. The probe was positioned 2.2-cm above the trap mouth (A), about even with the trap mouth (B), and 1.6-cm (C) and 1.0-cm (D) below the trap mouth.

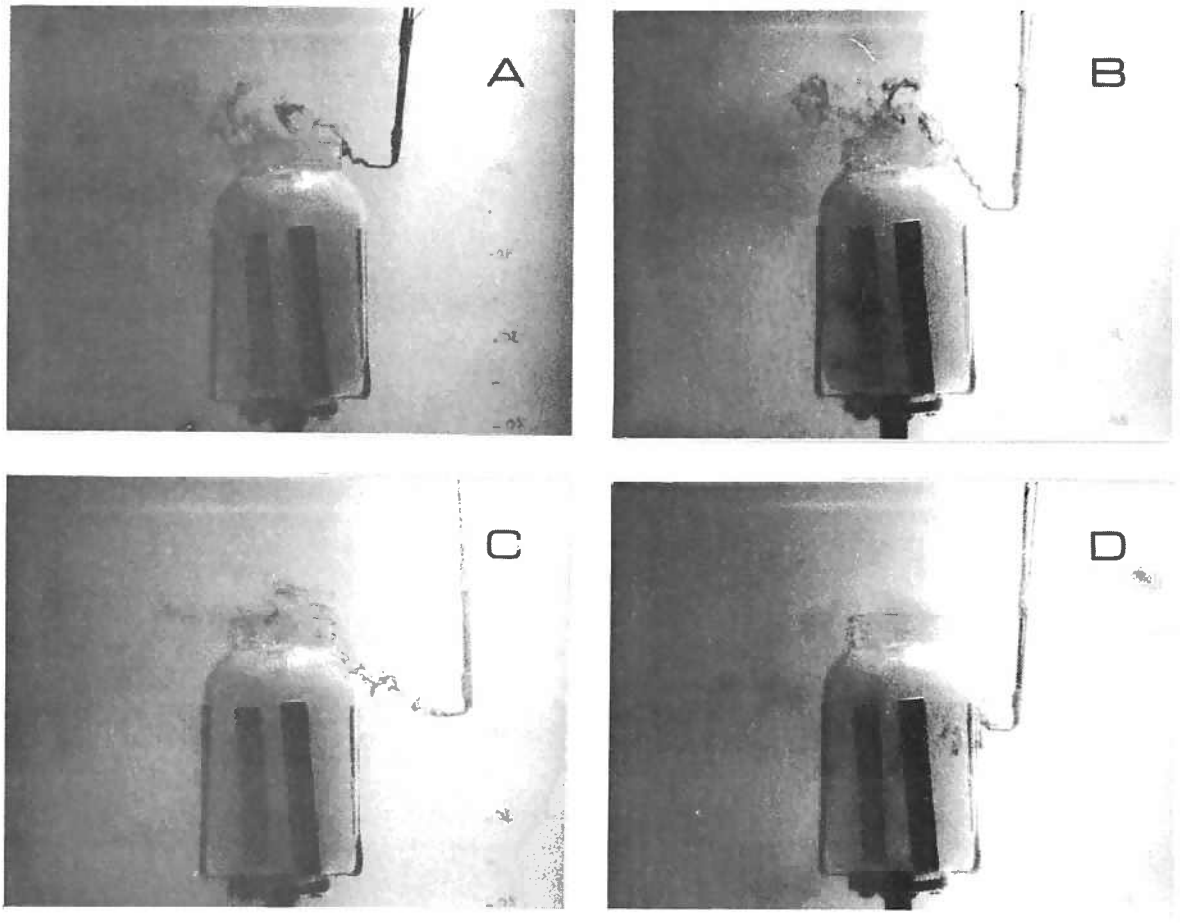


Figure 3.38: Visualization, using dye (see caption to Figure 3.17), of flow patterns below the mouth of a trap that was similar in design to trap OPG8.3-3.0. The dimensions of the trap pictured here are given in Figure 3.37. The flow is shown here moving from the right to the left of each frame. The probe was positioned 2.1-cm (A), 7.0-cm (B), 8.7-cm (C) and 11.4-cm (D) below the trap mouth.

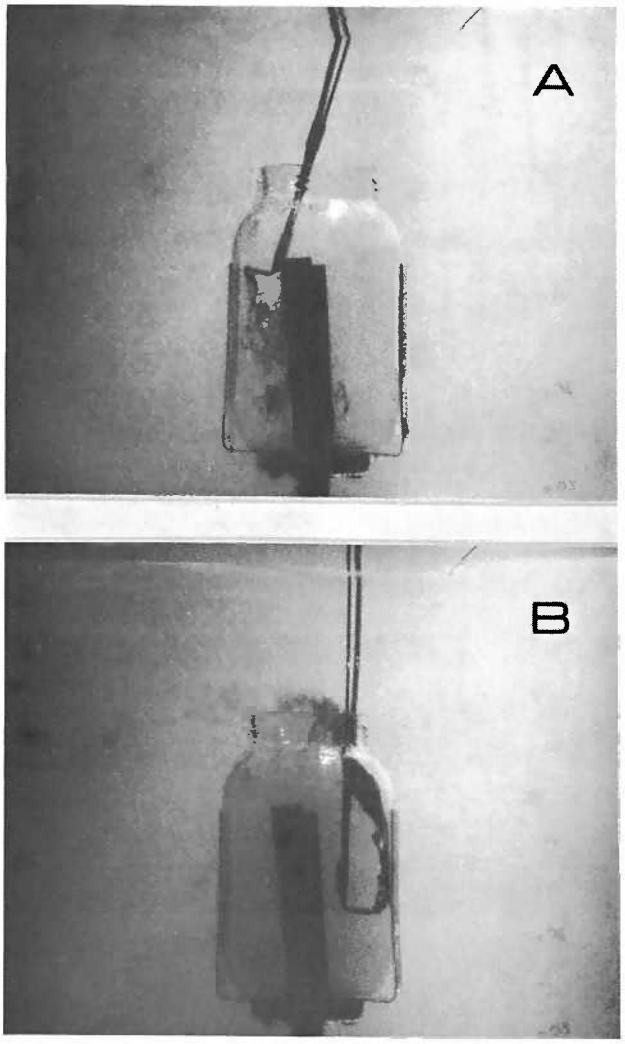


Figure 3.39: Visualization, using dye (see caption to Figure 3.17), of flow patterns inside a trap that was similar in design to trap OPG8.3-3.0. The dimensions of the trap pictured here are given in Figure 3.37. The flow is shown here moving from the right to the left of each frame. The probe was positioned 9.7-cm (A) and 17.8-cm (B) below the trap mouth.

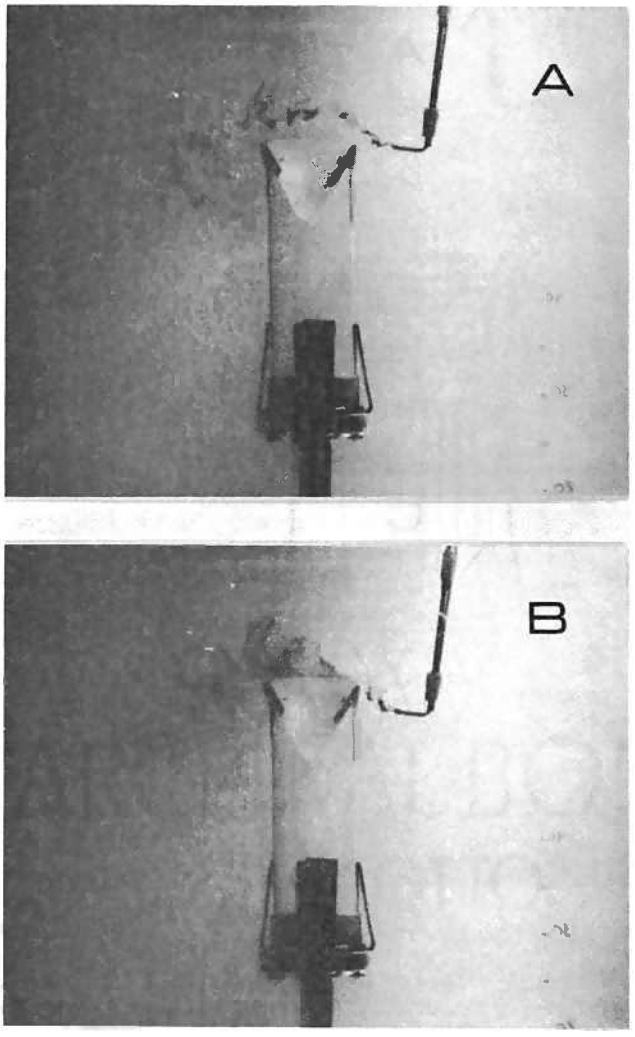


Figure 3.40: Visualization, using dye (see caption to Figure 3.17), of the flow near the mouth of trap TBC7.4-2.9 containing a funnel. The funnel inside the cylinder was 8.4-cm tall, 7.1 cm in inside diameter at the mouth, and 1.1 cm in inside diameter at the bottom. The flow is shown here moving from the right to the left of each frame. The probe was positioned about even with the trap mouth (A) and 2.1-cm below the trap mouth (B).

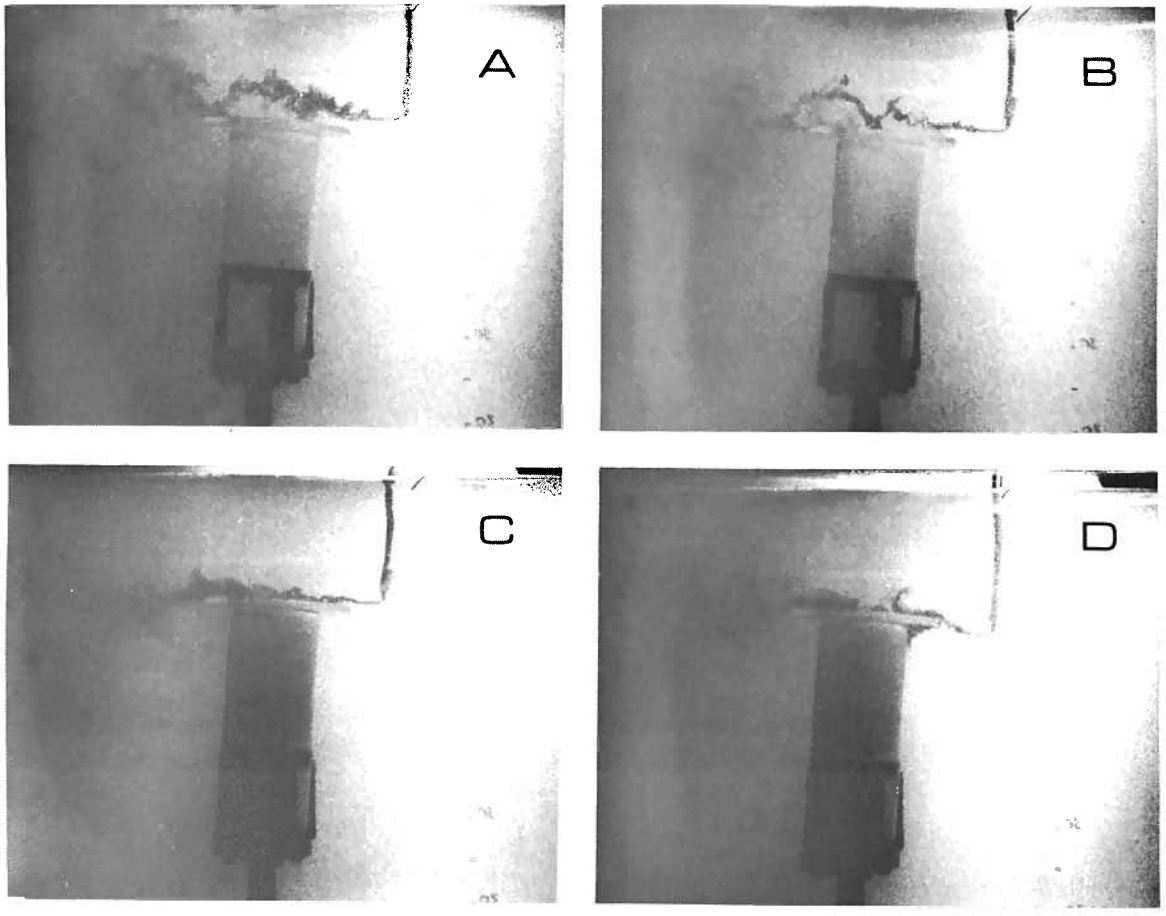


Figure 3.41: Visualization, using dye (see caption to Figure 3.17), of the flow near the mouth of trap OPP8.3-2.7. The flow is shown here moving from the right to the left of each frame. The probe was positioned about 1.0-cm (A), 1.3-cm (B), and 0.5-cm (C) above the trap mouth and about 1.0-cm (D) below the trap mouth.

TBC7.4-2.9, was unaffected by the presence of the trap (Figure 3.35A). However, dye streams released at heights approximately level with or 1-cm below the trap mouth were distorted as they passed over the trap (Figure 3.35B). At the leading edge of the trap the flow was displaced vertically up, while immediately downstream eddies dipped into the trap mouth. Hereafter, this phenomenon is referred to as "the shedding of eddies into the trap mouth." Dye was seen entering only the downstream inside perimeter of the trap mouth. This pattern of flow over the trap mouth was repeated for every cylindrical trap design tested with dye (e.g., see Figure 3.36A and B) and for the trap similar in design to trap OPG8.3-3.0 (Figures 3.37B, C and D). The most dramatic differences in flows over traps with larger mouth diameters was that the eddies shed over and dipping into the trap mouths were also larger in diameter (see Figure 3.36A and B, and Figure 3.37B, C and D). For the cylinders with small mouth diameters, that were tested with dye (traps TBC3.6-3.1 and TBC1.7-3.0), little eddies (less than the mouth diameter in size) were spun off into the trap and, occassionally, larger eddies (with diameters greater than the trap mouth diameter) were shed in the lee of the trap (pictures not shown).

To a depth of ~ 4.2-cm below the trap mouth, the cylindrical form of trap TBC7.4-2.9 deflected the flow up over the trap mouth (Figure 3.35C); again, flow entered the trap only through counter-clockwise eddies dipping into the downstream edge of the trap. However, flow at a depth of ~ 4.7-cm below the trap mouth (a distance equal to about a fifth of the total height of the trap) was deflected

sideways by the cylinder (Figure 3.35D); this flow did not pass over the trap mouth. The transition depth below the mouth, for which flow was no longer deflected upwards by the trap, was approximated for only one other trap design, the trap similar to OPG8.3-3.0. For this trap, flow was deflected upwards to a depth of ~ 8.7-cm below the mouth (see Figure 3.38B and C). At ~ 11.4-cm (or a distance of about a third of the trap height) below the trap mouth, the flow was deflected around the trap (see Figure 3.38D).

Inside trap TBC7.4-2.9, a single circulation cell of fluid was observed entering the downstream edge of the trap mouth, flowing straight down the backside of the cylinder, and then flowing straight up the upstream end of the cylinder (pictures not shown). This counterclockwise circulation cell was also observed in traps TBC14.7-2.9 and TBC14.7-1.6 (Figures 3.36C and D) and in the trap similar to OPG8.3-3.0 (Figure 3.39A and B). Dye was removed from the traps by scouring at the upstream edge of the trap mouth.

Flow over the mouth of a cylindrical trap (TBC7.4-2.9) containing a funnel was similar to flow over the other cylinder mouths; the flow was deflected up initially and then eddies were shed downstream (Figure 3.40A). However, the flow did not then penetrate straight down the back of the trap toward the bottom, but entered the downstream edge of the funnel and circulated back up the upstream edge. Very little dye entered the trap at all (Figure 3.40B).

Flow over the leading edge of the plate on trap OPP8.3-2.7 did not initially rise as much as over the other trap mouths. The flow tended to parallel the plate (Figure 3.41A, B, C and D). In addition

to counterclockwise eddies, it also appeared that clockwise eddies may have been shed over the trap mouth (see especially Figure 3.41D). Another striking difference between flow patterns near the mouth of this trap and the other designs tested with dye, was that a flow stream approaching the trap even at a height 1.0-cm below the mouth was partially deflected downward, below the plate (see Figure 3.41D). Flow entering at distances $\geq$ 2-cm below the trap mouth was completely deflected around the trap (pictures not shown).

3.4 Discussion

3.4.1 Accuracy and precision of fall velocity measurements

Replicate fall velocity measurements of perfect spheres (having a homogeneous and accurately determined particle density) falling through a perfectly still and unstratified fluid should result in measurement error due only to the accuracy and precision of the timing mechanism and to the accuracy of the measured distance over which the sphere falls. However, in this study the spheres were imperfect in both shape and density and the water column was not completely unstratified. Thus, the measurement precision estimated here using spheres includes the errors associated with chamber design (e.g., the extent to which the outside water bath maintains a homogeneous water viscosity in the inside water column), and chamber construction (e.g., the accuracy of the vertical distances between lines etched on the inside chamber walls), with the timing mechanism, and with imperfections in the spheres themselves.

The measurement precision for "best case" fall velocity

estimates (i.e., using spheres) sets the lower limit of "acceptable" error for fall velocity estimates under more variable conditions (i.e., using irregularly shaped particles such as larvae). For particles with similar W_m, the best precision was expected for measurements of spheres while lower precision was expected for irregularly shaped inert particles. Fall velocity estimates for larvae were expected to be the least precise because larvae are irregularly shaped, they often have spiny projections (e.g., the swimming larval setae in spionids) and they are composed of permeable tissue which may vary in density. In addition, measurement precision is expected to decrease with decreasing W_m because errors associated with timing the fall, with particle orientation during the fall, and with water column instabilities, are likely to increase.

The best case measurement error for the chambers was very low (< 1.0 percent) for spheres with relatively large W_m (0.826-2.80 cm/sec) and did not exceed 10 percent for spheres falling at speeds of 0.0566-0.0707 cm/sec in the small chamber and at 0.785 cm/sec in the large chamber (see Table 3.11). This error is, at least in part, due to water column instabilities. The within-runs measurement error for spheres tested in the small chamber varied between 0.6 and 12.3 percent, but higher values in this range occurred only when a focused light was used in the chamber (see Section 3.3.1). The focused light differentially warms the water in the upper half of the water column so that a larger temperature gradient is created. The temperature difference between 5-cm intervals is only 0.1 to 0.5°C and, thus, viscosity differences alone

TABLE 3.11

Summary of Between-Runs Precision of Replicate[1] Fall Velocity Measurements for Spheres, Irregularly Shaped Inert Particles and Larvae Tested in the Large and Small Chambers

Particle Type	Mean W_m [1] (cm/sec)	CV (percent)	Number[2] tested
Large Chamber			
spheres	0.826-2.80	0.2- 0.6	6
	0.785	7.3	1
irregularly shaped inert particles	2.01 -2.03[3]	0.7- 6.0[4]	3
	3.78 -4.29[5]	0.8- 1.5	2
larvae	0.163-0.182	7.9-21.9	4
Small Chamber			
spheres	0.0566-0.0707	4.4-10.0	4
larvae	0.0197-0.0548	5.2-26.0	13
	0.0408	39.5	1

1. At least three runs were made for each particle listed here, except where noted.
2. Number of different particles tested.
3. Sand grains.
4. Only two runs were made for each of two of the grains tested.
5. Macoma balthica fecal pellets.

are not sufficient to account for a 10 percent difference in W_m of a single sphere falling through the water column (from Stokes equation, ~ 4°C change in temperature is required to change fall velocity by 10 percent). However, these small temperature differences could cause water column instabilities and convection cells to develop. For example, during retrieval of a larva after a run (see Section 3.2.3), warm surface water could get pushed into the colder water near the bottom of the chamber; the gradual rising of this displaced warm water mass would create a water column instability. Even without the focused light, temperature gradients were measured in the inside water column because the outside water bath buffers the lower water column better than the surface waters (see Section 3.2.3). As the room temperature increases, the upper water cools faster than the bottom water; a convection cell would develop from the sinking of this slightly denser surface water.

Currents in convecting water masses with velocities of the order of particle W_m would displace a particle during a portion of its descent to decrease or increase (depending on the direction of the displacement) the local W_m; this results in within-runs measurement error. In addition, particles with relatively lower W_m are more likely to be affected by convection cells, if they occur. Variability in W_m between runs depends on the constancy of both the convection cell and the vertical path of a particle between replicate runs. A particle may encounter part of a convection cell during one run and not during another.

There was no evidence that within-runs measurement error

resulted from the spheres accelerating through the water column. That is, the 5-cm averaged vertical profiles of W_m indicated that the spheres reached terminal velocity before entering the first measurement interval because W_m did not systematically increase throughout any single fall. This result is supported theoretically for spheres settled in both chambers. By integrating the equation describing the force balance (submerged weight of the particle minus the drag force on the particle) on a sphere as it accelerates from the rest through a viscous fluid (i.e., neglecting inertial terms for low R_p), the time (T_r) required for the sphere to reach terminal fall speed can be estimated as

$$\frac{18\ \mu_f}{d^2 \rho_p} \cdot \tag{3.6}$$

For the plastic spheres ($d \simeq 220\ \mu m$, $\rho_p = 1.05\ g/cm^3$) settled under conditions in the small chamber ($\mu_f \simeq 1.0 \times 10^{-2}$ g/cm sec) $T_r \simeq 0.5$ sec and for glass spheres ($d \simeq 220 \mu m$, $\rho_p = 2.42\ g/cm^3$) settled under conditions in the large chamber ($\mu_f \simeq 1.3 \times 10^{-2}$ g/cm sec) $T_r \simeq 0.09$ sec. Multiplying T_r by W_m for the spheres gives the vertical distance required for the spheres to reach terminal velocity; this distance is $\simeq 3.5 \times 10^{-3}$ cm for plastic spheres in the small chamber and $\simeq 1.8 \times 10^{-1}$ cm for glass spheres in the large chamber. The first timing mark in the small chamber is ~ 5-cm below the water surface and in the large chamber this mark is > 15-cm below the water surface so, clearly, all particles should have reached terminal velocity before the timed portion of their falls.

Comparisons between W_m and W_c, fall velocities calculated either from Stokes equation for $R_p \leq 1$ or from a fall velocity curve (Grant, 1977; a curve similar to Rubey's empirical relationship near the Stokes range) for $R_p \geq 1$, for the spheres settled in both chambers are presented in Tables 3.3 and 3.4. In 10 of the 12 comparisons, the measured fall velocities were, on the average, within 10.2 percent (SD = 6.4 percent, range = 1.3 to 22 percent) of the calculated values. A 10 percent difference between measured and predicted values for fall velocities of spheres is excellent, compared to other studies of spheres with R_p of the order 10^0 (e.g., see Gibbs [1972]), considering the possible sources of inaccuracy in sphere shape and density alone. However, in two comparisons (the two red plastic spheres settled in the large chamber), W_m and W_c were radically (by 637 and 8639 percent) different. Because these results are so deviant from the others, it is probable that the vial containing the red plastic spheres was labeled with the wrong value of ρ_p.

In the present study, direct comparisons of precision estimates for spheres, irregularly shaped inert particles and larvae are complicated because, (1) all the inert and living particles did not have similar fall velocities; W_m spanned two orders of magnitude for the particles tested, and (2) different particles were tested in the large and small chambers. Thus, the precision estimates determined here must be considered approximate figures and not exact values of the precision of the technique.

The expected relative measurement precision for spheres, for

irregularly shaped inert particles, and for larvae generally was supported by the fall velocity data collected in both chambers (these data are summarized in Table 3.11). The between-runs error for sphere fall velocity measurements was less than the error for larval fall velocity measurements by a maximum of two orders of magnitude in the large chamber and one order of magnitude in the small chamber. In the large chamber, error estimates for irregularly shaped inert particles fell between error estimates for spheres and error estimates for larvae. In addition, all of the data indicate that error increases with decreasing W_m.

The spheres tested in the small chamber provided relatively accurate estimates of best case measurement error for the larvae tested because W_m for these spheres (0.0566-0.0707 cm/sec) covered the middle of the range of W_m for the larvae (0.0135-0.1150 cm/sec, see Table 3.7). Thus, a conservative 10 percent of the imprecision in replicate larval fall velocity measurements can be attributed to the measurement technique alone. The possible sources of the remaining ~ 15 percent (in one case, 30 percent) error for larval fall velocity measurements will be discussed subsequently.

The spheres tested in the large chamber probably underestimate the best case measurement error for the larvae tested because W_m for these spheres (0.785-2.80 cm/sec) were at least an order of magnitude larger than W_m for the larvae (0.084-0.298 cm/sec, see Table 3.6). An approximately 10 percent best case measurement error may also be appropriate for this chamber. The increased error associated with timing falls in the large chamber over twice the

vertical distance (50 cm) as in the small chamber (25 cm) is assumed to be roughly balanced by the relatively large W_m (by about a factor of two, see Tables 3.6 and 3.7) for larvae tested in the large chamber. Thus, a maximum of ~ 12 percent of the imprecision in replicate larval fall velocity measurements is due only to characteristics of the larvae.

A between-runs measurement error for larvae of ~ 15 percent is actually lower than expected when the possible sources of variability in these fall velocity measurements is evaluated. In fact, all of the variability can be accounted for by changes in the orientation of larvae during their falls. Even though the cup-shaped concave-up orientation (see Figure 3.1) appeared to be the most common during falls in the large chamber, no quantitative estimates were made of the proportion of the time larvae actually fell like this. The drag on a solid body falling through a fluid at low R_p is due primarily to the frictional drag on the surface area of the body. Larvae falling in the cup-shaped concave-up orientation roughly approximate a sphere in their frontal surface area, so narcotized length was used to plot the data (e.g., see Figure 3.16). Narcotized length is actually an estimate of the maximum cross-sectional length exposed during a fall, while narcotized width represents the minimum exposed dimension. The narcotized width was about a third of the narcotized length for most larvae (see Tables 3.6 and 3.7). For spherical particles falling in Stokes range ($R_p < 1$), the drag coefficient (C_D) is inversely related to particle diameter (see eqs. 3.3 and 3.4) and fall velocity (W_c) is inversely related to the square of

particle diameter and, thus, particle surface area (see eq. 3.5). Thus, the theoretical fall velocity of a sphere with diameter = d and with diameter = 3d would differ by ~ 900 percent.

The orientations of swimming setae and other spiny projections on larvae during their falls could have even a larger effect on fall velocity. Hutchinson (1967) reviewed the fall velocity measurements made on freshwater plankton, such as the cladoceran, Daphnia. An ~ 70 percent reduction in sinking speed occurred when the two anterior antennae of Daphnia were fully extended versus folded together (in the study of Eyden 1923, cited by Hutchinson 1967) and a 22 percent increase in sinking speed occurred when the lateral spines were removed from outspread antennae (in the study of Hantschmann 1961, cited by Hutchinson 1967). Results of the present study also indicated that fall velocity is related to the larval form. The presence of the long swimming setae on the west coast (Mission Bay) Streblospio benedicti may have contributed to its lower W_m compared to east coast (MERL) S. benedicti, that do not possess these swimming setae (see Table 3.7).

Summing all the variables in fall velocity related to just the form of the larvae as it falls, clearly a 15 percent imprecision in the data is reasonable. In fact, not only would the between- and within-runs error in W_m probably have been less if a more precise measurement was made of the larval frontal surface area exposed during a given fall interval, but a stronger correlation between larval size and larval fall velocity also might have occurred. Alternatively, an estimate of the average cross-sectional dimension

exposed during a fall (e.g., by the method of Janke, 1966, using the cube-root of the product of the longest, shortest and intermediate dimensions) might improve both the error in fall velocity estimates and the correlation between larval size and fall speed.

Equally as critical as estimates of the precision, are estimates of the accuracy of larval fall velocity measurements. The techniques for estimating fall velocity in the present study appear to be accurate to ± 10 percent, as evidenced by the agreement between the predicted theoretical and measured fall velocities of spheres (see Tables 3.3 and 3.5). It is not possible to calculate meaningful theoretical fall velocities for larvae because the density (ρ_p) of the organisms is unknown and because the frontal surface area presented during a fall may change continually. However, because the drag coefficients for irregularly shaped particles with low R_p (< 2.0 in the study of Baba and Komar, [1981b]) follow Stokes' law, as long as the proper corrections are made for particle shape (e.g., see Baba and Komar [1981b]), larvae with low R_p also should have drag coefficients as defined by Stokes' equation and corrected for shape. In other words, the accuracy should be similar for fall velocity estimates of all low R_p particles measured by the techniques used in this study. (Note also that a straight line through the larval fall velocity measurements plotted in Figure 3.16 would approximately parallel the lines for the inert particles plotted in this figure, indicating that the larvae probably are falling like Stokes' particles.) However, there is one possible source of inaccuracy inherent to larval fall velocity measurements and not to the

measurements for inert particles; the density (ρ_p) of live organisms may change as a result of the anesthetizing procedure. Thus, if ρ_p of "narcotized to death" larvae is similar to ρ_p for live individuals then the accuracy of fall velocity measurements for larvae and inert particles also should be similar.

Replicate larval fall velocity measurements gradually decreased with time since the narcotizing treatment began (e.g., see Figures 3.14 and 3.15) indicating that ρ_p of larvae may change as a result of the anesthetizing procedure. The "narcotizing to death" procedure may cause tissue to become increasingly more isotonic with time since the treatment began. The largest change in W_m took place within 40 min of treatment, in most cases. For 10 larvae where the first and second runs began 10- to 25-min and 28- to 43-min, respectively, after the treatment began, W_m decreased by an average of 1.3 percent per minute (range = 0.14 to 3.1 percent per minute, calculated as

$$\frac{W_m \text{ first run} - W_m \text{ second run}}{W_m \text{ first run}} \times 100).$$

All larvae in the large chamber and 85 percent (22 out of 26) of the larvae in the small chamber were tested from 7- to 40-min after the treatment began (Tables 3.6 and 3.7). Assuming the 1.3 percent per minute rate of change in W_m is relatively constant within the first 40-min since treatment began, larval fall velocities measured in this study could be underestimates, on the average, by 23 percent (SD = 9 percent, range = 6 to 52 percent for N = 28). The fall

velocity measurements for four of the six MERL Streblospic benedicti were made 52- to 137-min after treatment began (Table 3.7). These fall velocity estimates could be low by 68 to 178 percent, if the 1.3 percent per minute average rate of change in W_m is used in calculations. However, the measured fall velocities probably are not this inaccurate since the percent rate of change in W_m tended to decrease with time since treatment began (e.g., see Figures 3.14 and 3.15); the 1.3 percent per minute rate of change is probably not applicable over the entire 52- to 137-min intervals.

An average inaccuracy in larval fall velocity measurements of 23 percent due to possible density changes in narcotized tissues, added to the average inaccuracy of 10 percent (determined for spheres) due to all other aspects of the measurement technique gives an overall average inaccuracy of 33 percent. However, this figure is challenged by the four Mission Bay Streblospic benedicti larvae with first run 5-cm averaged fall velocities that were 63 to 343 percent higher in intervals in the upper water column than in intervals near the bottom (see Table 3.8). It is possible that these larvae physiologically resisted tissue degradation longer than other larvae so that the anamolously high values for W_m may, in fact, be the accurate estimates. Alternatively, the narcotizing procedure may have been less effective with these larvae; the high W_m values may have resulted from active swimming or active sinking by the organisms. The fact that two of these larvae were observed moving or beating their cilia after the first run supports the second hypothesis. Another explanation for these unusually high fall velocities is that

the larvae did not passively sink over these intervals, but were displaced vertically by a hydrodynamic phenomena (such as a convection cell).

The precise effects of the narcotizing treatments on the physiology and density of the organisms require rigorous experimental investigation. This research was outside the scope of the present study. The goal of this investigation was to obtain a range of values for larval fall velocities so that passive particles having fall velocities with this range could be selected for use in the flume study. Certainly this goal was achieved. In fact, given an imprecision of ~ 10 percent in the measurement technique alone, an added imprecision of ~ 15 percent for tests of larvae, an average inaccuracy of 10 percent for the technique, and an added average inaccuracy of 23 percent for tests of larvae, it is surprising that the measured fall velocities are scattered over only one order of magnitude (see Figure 3.16). In fact, the W_n values estimated here are within the error bars of the one body length per second fall velocity relationship summarized by Rudyakov and Tseytlin (1980) for pelagic organisms ranging from 5×10^{-3} to 10^2 mm in length.

A maximum overall error in larval fall velocity measurements of 58 percent produces variation in the data that is within the range of the variation observed in other studies where fall velocities of nonspherical particles were measured. The variability in measured fall velocity for larvae of a given narcotized length ranges from 22 to 68 percent generally decreasing with increasing fall velocity (Table 3.12). This variability is remarkably similar to the percent

variation in fall velocities of nonspherical inert particles of a given size, as measured in other studies (these data are summarized in Table 3.12). A percent variation of 49 to 60 was observed for particles of a given size falling between 0.030 and 0.140 cm/sec (copepod fecal pellets in the study of Small et al., 1979). Within a study and between the studies, the percent variation decreased for increasing fall velocities. Thus, the techniques used here to estimate larval fall velocities were reasonably precise and accurate for the state-of-the-art in particle fall velocity measurements.

3.4.2 Measured larval fall velocities and particles used to seed the flume flow

The two bead mixtures selected for seeding the flume flow had theoretical fall velocities (W_c) within the range of those measured for polychaete larvae (see Figure 3.16). The fall velocities of ~ 94 percent of the 25-μm mixture spanned most of the range of measured larval fall velocities; only larvae falling from 0.2 to 0.3 cm/sec (~ 23 percent of the larvae tested) were not represented by this mixture. Fall velocities (0.0501 to 0.0575 cm/sec) of a 24.8-μm bead (the mean bead diameter for the 25-μm mixture) in 22 to 28°C freshwater (conditions during trap tests using this mixture, see Table 3.10) were slightly higher than the mean fall velocity (0.0477 cm/sec, SD = 0.0234 cm/sec, N = 27) for all larvae tested in the small chamber. The fall velocities of ~ 97 percent of the 46-μm mixture spanned only the high end of the measured larval fall velocities; larvae falling at speeds $\leq$ 0.1 cm/sec (~ 67 percent of the larvae tested) were not represented by this mixture. Fall

TABLE 3.12

Comparison of Measured Fall Velocities of Nonspherical Particles from a Variety of Studies

Reference	Type of particle	Particle shape	Units of size	Approximate particle size	Approximate range in fall velocity[1] (cm/sec)	Percent variation in fall velocity[2]
Present Study[3]	polychaete larvae	usually cup-shaped during fall (see Section 3.3.2 and Fig. 3.1)	NL (see Fig. 3.1) (μm)	350 550 750 950	0.013-0.062 0.040-0.21 0.086-0.32 0.165-0.26	66 68 58 22
Small et al. (1979) replotted in Komar et al. (1981)	mixed small copepod fecal pellets	cylindrical	$L^2(L/D)^{-1.664}$ (cm^2) where L = pellet length and D = pellet diameter	4.5×10^{-5}	0.030-0.12	60
	copepod fecal pellets of Anomalocera patersoni	cylindrical	same as above	1.3×10^{-4}	0.048-0.14	49
Fowler and Small (1972) replotted in Komar et al. (1981)	euphausiid fecal pellets	cylindrical	same as above	3.3×10^{-3}	0.32-0.76	41
Fok-Pun and Komar (1983)	planktonic foraminifera shells of Globigerinoides sacculifer	ellipsoidal	D_n = (μm) $(D_S D_i d_1)^{1/3}$ where D_S, D_i and D_1 are the shortest, intermediate, and longest diameters, respectively	40	1.0-2.3	40

TABLE 3.12 (cont. -2)

Reference	Type of particle	Particle shape	Units of size	Approximate particle size	Approximate range in fall velocity[1] (cm/sec)	Percent variation in fall velocity[2]
Fok-Pun and Komar (1983 - cont.)	planktonic foraminifera shells of Globorotalia hirsuta	ellipsoidal	same as above	50	1.6-2.3	18
	planktonic foraminifera shells of Orbulina universa	spherical	D_i = intermediate diameter (μm)	40	1.8-4.0	38
Baba and Komar (1981a)	natural quartz sand grains	irregular	same as above	50	4.8-7.0	18

1. In all the studies, the fall velocity measurements for a given size were either all made at the same temperature or the values were normalized to a particular water viscosity, as in the present studies. However, the fall velocities are not strictly comparable between studies because different normalizing factors were used.
2. Calculated as half of the range, and as a percentage of the mean value.
3. The data are plotted in Figure 3.16.

velocities (0.167 to 0.179 cm/sec) of a 46.4-μm bead (the mean bead diameter for the 46-μm mixture) in 20 to 23°C freshwater (conditions during trap tests using this mixture) were slightly lower than the mean fall velocity (0.209 cm/sec, SD = 0.077 cm/sec, N = 16) for all larvae tested in the large chamber.

Larvae with 8.79×10^{-4} cm/sec $< W_n \leq 0.225$ cm/sec are falling in the "silt" range for spherical quartz particles sinking in 20.4°C, 30 ppt seawater. W_n for 82 percent of the larvae tested clump at the upper end of this silt range. The approximately one order of magnitude in larval fall velocities is a relatively small spread compared to the nearly three order of magnitude range in fall velocities for silts. Larvae with W_n between 0.224 and 0.517 cm/sec are falling like "very fine sand" in the 20.4°C, 30 ppt seawater. 17 percent of the larvae tested were falling in this range.

3.4.3 Accuracy and precision of particle collection efficiency estimates

Determining the errors associated with each term involved in calculating trap collection efficiencies (E, see Section 3.2.7) allows estimates of "acceptable" variability (or of the overall measurement error) in collection efficiencies for replicate tests of a single trap design. The expected amount of variability for all aspects of the techniques used in this study is determined in this way. This information is necessary for evaluating significant differences among mean collection efficiencies of the various trap designs. The precent CV for mean collection efficiencies in replicate tests of a given trap design are not expected to be lower

than the overall measurement error. For example, mean collection efficiencies for two trap designs must differ by at least twice the overall measurement error to be considered biased collectors, with respect to each other. If the actual variability in replicate collections by a single trap design is greater than the expected amount, then the hydrodynamic characteristics of the trap as a collecting device must be contributing to this variability. For these traps, the actual error bars (one SD around the mean) for replicate collections set the limits for statistically significant differences between trap designs.

The approximate errors associated with each term used to calculate E are given below. In most cases, the average errors are calculated for a specified range of conditions. Whenever possible, the minimum and maximum values of the error terms also are provided. Exact error estimates require separate calculations for each individual trap tested because the precise values of each error term depend on trap size (month diameter and volume), the concentration of particles in the water during a trap collecting interval, and the actual weight of particles collected by a trap. However, the purpose of the error analysis present here is to provide only a rough estimate of the overall precision of the techniques used to determine trap collection efficiencies in this study. While the sensitivities of the various error terms to characteristics of the trap tested and conditions during a trap test are briefly discussed here, experimental results that may be explained by measurement errors substantially different from those estimated in this section are

discussed later (Section 3.4.3, 3.4.4, and Appendix II).

T_i, the length of the trap collecting interval, was approximately timed with a stopwatch accurate to ± 0.1 sec. T_i was always considered to be 510 sec for calculations, but the actual length of each trap collecting interval was not determined exactly. Standardized procedures for capping and uncapping traps in the flume minimized error in this term so that collecting intervals probably did not vary by more than ± 5 sec.

A_t, the trap mouth area, was calculated from trap diameters measured with a ruler accurate to ± 0.05 cm. Replicate traps for six of the trap designs did not vary at all in their inside diameters and replicate traps for all other designs varied by only ± 0.1 cm (see Table 3.1). The largest imprecision would be for the 8.3-cm diameter traps (OPF8.3-1.9 and OPP8.3-2.7), and the smallest error for the 14.7-cm diameter trap (OPF14.7-1.9).

C_i, the mean bead concentration during a trap collecting interval, was calculated as C_{ap}-C_{bp}, where C_{ap} = the mean concentration of all particles sampled during a trap collecting interval and C_{bp} = the mean background particle concentration for that particular series. Two sources of imprecision for each concentration measurement were, (1) errors in measuring the water volume in the sample and (2) errors associated with weighing the Millipore filter containing particles from the sample. The accuracy of the microbalance used to weigh samples of particles collected on Millipore filters (Section 3.2.5) was at least ± 0.001 mg and the accuracy of the 250-ml graduated cylinders used to determine sample

volume was about ± 0.05 ml. Sample volume was measured to ± 1 ml for all samples $\leq$ 250 ml. The largest source of error in filter weights was the humidity correction factor, resulting in average errors of ± 0.14 mg for each filter weighted (this value was derived in Section 3.2.5). The total error in each concentration estimate depends on the total weight of particles collected in the sample and on the exact sample volume.

For C_{ap}, the weight of total particles per filter, ranged from about 1.5 to 3.0 mg and sample volumes ranged from about 200 to 250 ml. Thus, for an average concentration of 2.25 mg/0.225 l = 10 mg/l, the maximum error would be ± 0.72 mg/l. For particle concentrations of 8 mg/l, the error could be as high as ± 0.74 mg/l and for concentrations of 12 mg/l, the error could be as low as ± 0.51 mg/l.

For C_{bp}, the weight of total particles per filter ranged from about 0.1 to 0.4 mg and sample volumes also were approximately 200 to 250 ml. An average concentration of 0.225 mg/0.225 l = 1.0 mg/l yields a maximum error of ± 0.64 mg/l. For concentrations as small as 0.5 mg/l, the error is as high as ± 0.71 mg/l; a minimum error of ± 0.55 mg/l is associated with concentrations of 1.6 mg/l.

The total error in C_i is calculated as the total error in C_{ap} minus the total error in C_{bp}. For the average conditions given above where C_{ap} = 10 ± 0.72 mg/l and C_{bp} = 1.0 ± 0.64 mg/l, the average error (for all possible combinations of the error terms) for C_i = 9.0 mg/l is ± 0.72 mg/l (or 8 percent).

If this average error of 8 percent is a reasonable estimate,

then the actual variability about the C_i values calculated for each trap collecting interval should reflect a similar average percent error. For 83 trap collecting intervals in the 7/10/82, 7/22/82 and 8/24/82 series, the mean CV was 4.9 percent (SD = 2.9 percent); CV ranged from 0.8 to 15.4 percent, but only five out of the 83 values were > 10 percent. Thus, the error in C_i calculated here is higher than the measured mean percent error, but is still within the range of the measured values.

W_c, the fall velocity of the beads, was not measured in this study, but was calculated using Stokes equation (see Section 3.2.5). For each trap collecting interval, W_c was calculated for the mean bead diameter (24.8 or 46.4 μm) of the bead mixture used to seed the flow, using a viscosity value for the approximate (to 0.1°C) water temperature during that interval (see Section 3.2.7). The possible sources of inaccuracy in these calculations are errors in estimating the particle density, the particle sphericity, and the water viscosity and density. There is no way to determine the true inaccuracy of the calculated values, but measured fall velocities of spherical particles are usually within 10 percent of Stokes values (e.g., see Table 3.5 and 3.7, and Section 3.4.1). This is the minimum error associated with W_c. Approximate errors are calculated here for W_c of 24.8- and 46.4-μm beads in freshwater temperatures representing the midpoints of the ranges in temperatures for all series that used the particular bead mixture (see Table 3.10). Thus, W_c = 0.0525 ± 0.0052 cm/sec for a 24.8-μm bead falling through 24°C water and W_c = 0.171 ± 0.017 cm/sec for a 46.4-μm bead

falling through 21°C water.

A potentially much larger source of error in W_c arises from using W_c for only the mean bead diameter when a spectrum of bead sizes were actually available to and collected by traps. The absolute efficiency of a given trap design represents the ability of the trap to estimate the true flux of particles through the water column. Such absolute efficiencies can be calculated accurately only by integrating the separate efficiencies of particle collection for the continuum of particle sizes present in the flow and collected by the traps. The error associated with calculating "mean bead diameter" efficiencies and not absolute efficiencies in this study is evaluated here for two cases: (1) where traps collect particle sizes in proportion to their availability, and (2) where traps differentially collect certain particle sizes over others (see Sections 2.3.2 and 2.4.3).

Even though both bead mixtures used in this study had unimodal particle size distributions, as determined by the Coulter Counter (see Figure 3.5), W_c for ~ 94 percent of the beads in the 25-μm mixture spans a range of about one order of magnitude (from 0.0144 cm/sec to 0.205 cm/sec, see Figure 3.16) and W_c for ~ 97 percent of the beads in the 46-μm mixture varies by a factor of about four (from 0.080 cm/sec to 0.340 cm/sec, see Figure 3.16). Thus, the maximum error associated with using W_c for only the mean bead diameters in the mixtures is 180 percent for the 25-μm mixture and 70 percent for the 46-μm mixture. If the size distribution of particles in the flow and in the traps is similar to the distributions measured by the Coulter Counter (the first case

mentioned above), then the "mean bead diameter" efficiencies calculated in this study are inaccurate in an absolute sense, but the errors associated with the calculated efficiencies are consistent between all traps tested. Absolute efficiencies would not change the collection efficiencies of the trap designs relative to each other. If all bead sizes are not available to the traps in the proportions given in Figure 3.5, and/or if the traps differentially collect certain bead sizes over others (the second case mentioned above), the 70 to 180 percent errors in W_c could be realized in these experiments.

It is impossible to determine precisely which case occurred in the present study because the size distributions of beads in water samples or in trap samples were not measured. However, the available information (given below) indicates that the first case was the most likely alternative. Bead sizes in the water column were probably well-mixed because bead concentrations varied randomly with height above the bed (see Figure 3.19). In addition, the proposed mechanism by which a trap could differentially select for certain particle sizes (see Section 2.4.3) may not distinguish between particles that differ in fall velocities by only a factor of three or even by an order of magnitude. That is, particles will be retained in an eddy if $W < \omega$, where W = particle fall velocity and ω = the angular velocity of the eddy. Thus, the determining value of W for retained versus nonretained particles would have to lie within the relatively small ranges in particle fall velocities for the bead mixtures used here (fall velocities of natural silt particles, for

example, span three orders of magnitude, see Section 3.4.2). This is unlikely; however, until ω for eddies shed by various trap designs or the bead sizes in the water column and in traps are actually measured, the possibility of particle size selection by traps for the ranges of particle sizes used in this study cannot be discounted completely.

Absolute collection efficiencies were not calculted here because only relative differences in collections between the various trap designs were necessary for testing the hypothesis that larvae are collected like passive particles. Thus, for the purposes of this study, the ~ 10 percent error associated with calculating W_c for the mean bead diameter in a mixture using Stokes equation, is the appropriate error estimate for replicate trap tests. Differential particle size selection by traps is acknowledged as a potential mechanism to account for large differences in efficiencies between trap designs.

The total error for B_p, the predicted weight of beads collected by a trap, is calculated using all possible combinations of the errors associated with each term in the equation $B_p = (T_i)\ (A_t)\ (C_i)\ (W_c)$. Thus, a total error in B_p is calculated for $T_i = 510 \pm 5$ sec, $A_t = 54.11 \pm 1.31$ cm^2, $C_i = 9.0 \pm 0.72$ mg/10^{3}cm^3 and $W_c = 0.0525 \pm 0.0052$ cm/sec for a 24.8-μm bead and $W_c = 0.171 \pm 0.017$ cm/sec for a 46.4-μm bead. For the 24.8-μm bead, $B_p = 13.04$ mg with an average error of $\pm$ 1.36 mg (or 10.4 percent); the maximum error is $\pm$ 2.99 mg (or 22.9 percent) and the minimum error is $\pm$ 0.03 mg (or 0.2 percent). For the 46.4-μm

bead, B_p = 42.47 mg with an average error of ± 4.39 mg (or 10.4 percent); the maximum error is ± 9.69 mg (or 22.8 percent) and the minimum error is ± 0.14 mg (or 0.3 percent). Note also that these are the approximate errors for a trap mouth diameter of 8.3-cm ± 0.1 cm.

B_t, the weight of beads collected by a trap, was calculated as B_f (the final measured weight of beads in a trap) minus B_w (the calculated weight of beads contained in the volume of water initially collected by the trap). The inaccuracy in B_f is due only to errors in the microbalance, which is accurate to at least ± 0.001 mg. The imprecision in B_f is due only to the humidity correction factor of ± 0.14 mg for filter weights. The weight of particles collected per filter varied between about 1.0 and 71.5 mg. Because the same average imprecision associated with the humidity correction factor exists for each filter weighed, a proportionally much larger error occurs for the smaller particle weights.

B_w is calculated as (C_{ap}) (V_t); the average error for C_{ap} was previously determined to be ± 0.72 mg/l for C_{ap} = 10 mg/l. The error in V_t depends on the measured trap volume. Volume inaccuracy depends on the size of graduated cylinder used to measure the sample: a 250-ml cylinder is accurate to about ± 0.05 ml, a 500-ml cylinder to about ± 0.1 ml and a 1000-ml cylinder to about ± 2.5 ml. The imprecision in V_t is also dependent on sample volume because samples < 250 ml in volume were measured to ± 1 ml (with a 250-ml cylinder), samples from 250 to 500 ml in volume were measured to ± 2.5 ml (with a 500-ml cylinder) and samples > 500 ml in volume

were measured to ± 5 ml (with a 1000-ml cylinder). The largest potential error in V_t is 8.3 percent, for the smallest trap volume of 12 ml measured to ± 1 ml. The percent error for all other trap volumes was < 1.0 (calculated for the trap volumes listed in Table 3.1 and the errors listed above). Thus, the average error in B_w = 0.12 mg for C_i = 10 ± 0.72 mg/l and the smallest trap volume of 12 ± 1 ml, is ± 0.01; the average error in B_w = 14.50 mg for C_i = 10 ± 0.72 mg/l and a larger trap volume of 1450 ± 5 ml is ± 1.04 mg. The average total error in B_t for these two examples is B_t = 0.88 ± 0.14 mg (or 14.9 percent) for the smallest trap volume (if B_f = 1.0 ± 0.14 mg) and B_t = 15.50 ± 0.88 mg (or 5.7 percent) for the larger trap volume (if B_f = 30 ± 0.14 mg).

Another potential source of error in B_t is background particles that sink into a trap. B_t is calculated assuming that the background particles represent an insignificant portion of the total vertical flux of all particles in the flume. Assuming that the background particles are too light to fall into traps during the 8.5-min collecting intervals, then these particles would be present only as part of B_w. To test this assumption, unseeded flume water was circulated at the maximum pumping rate for a 9-hr period and sampled hourly for background particle concentrations. Particle concentrations remained at ~ 1.0 mg/l (± 0.5 mg/l) during the entire 9-hr period. However, when the flow was continuously seeded with the 25-μm bead mixture for ~ 5 hr and then allowed to circulate unseeded, particle concentrations decreased at a rate of ~ 10 mg/l per hour. These results suggest that the background particles are not falling

out of the water over the length of the flume or, if they do settle to the bottom, they are much more easily resuspended by the flow than are particles in the 25-μm bead mixture. This steady state in background particle concentrations justifies the procedure used here in correcting trap samples for background particles in the flow.

To roughly estimate the total error in E (= B_t/B_p), the trap collection efficiency, the following example is used: an 8.3-cm diameter trap with a volume of 1450 ml (see Table 3.1, this is trap OPP8.3-2.7) collecting in 24°C freshwater seeded with the 25-μm bead mixture at C_i = 9.0 mg/l. This example represents roughly average conditions for all terms involved in calculating E. For E = 1.16, the average error is ± 0.13 or 10.9 percent, for all possible combinations of the error terms of ± 1.39 mg for B_p = 13.36 mg and of ± 0.88 mg for B_t = 15.50 mg. The total range of percent error in E for this example is 4.7 to 18.0. If the 46-μm bead mixture was used and B_f = 60 ± 0.14 mg, then the average error is ± 0.11 for E = 1.07 (or 10.2 percent); the range in percent errors would be 7.2 to 13.5.

Thus, a reasonable estimate for the total measurement error in calculating E is roughly 10 percent (± 5 percent), for average conditions during trap tests. This average measurement error could be as large as ~ 20 percent for the smallest traps tested (because the average error in B_t increases by ~ 10 percent), but the average measurement error probably does not decrease to much less than ~ 5 percent for the largest traps tested (because the average error of ~ 10 percent in B_p is still present even when the average error in

B_t decreases).

3.4.4 Measured particle collection efficiencies: variability between replicates and between series

The variability around the mean E_r values calculated for all traps tested in this study ranged from CV = 0.1 percent to CV = 42.0 percent (mean = 16.1 ± 9.7 percent for N = 37, see Appendix III). This average 16 percent imprecision is higher than the average total measurement error of 10 percent, calculated in Section 3.4.3, but is within the predicted 5 to 20 percent total range in measurement error. However, the CV for the mean E_r values of over a third of the traps tested was between 20 and 42 percent suggesting that factors, other than just those included in measurement-error calculations, contributed to the variability in replicate particle collections by these trap designs.

A close examination of the raw data in Appendix III suggested an additional source of variability in replicate collections (described below) that could not be included in the measurement-error calculations. For a given trap design, values of E_r appeared to decrease over the time course of a series. This trend was tested for trap collections during each series and for all series combined, using Mosteller's test of predicted order; the replicate E_r values for a given trap design were ranked in relation to the time, during the series, that the replicate collection took place. Binomial probabilities that the predicted order 3-2-1 (from highest to lowest E_r value over the time course of a series), would occur the observed number of times, by chance alone, are listed in Table 3.13.

TABLE 3.13

Results of Statistical Tests[1] of the H_0 that E_r Values of a Given Trap Design Decrease During the Time Course of a Series

Series	Total Duration of Trap Tests (hr)	Occurrence of Predicted Order[2]	Total Number of Traps	Binomial Probability	Significance Level
6/7/82[3]					
270 min	1.3	0	4	0.482	NS
390 min	1.4	1	4	0.386	NS
510 min	2.1	3	4	0.015	$\alpha \leq 0.05$
6/24/82	6.0	6	12	0.007	$\alpha \leq 0.01$
7/10/82	4.9	2	6	0.201	NS
7/22/82	5.0	1	7	0.326	NS
8/24/82	7.8	5	13	0.038	$\alpha \leq 0.05$
All series combined		18	50	0.0005	$\alpha \leq 0.001$

1. Mosteller's nonparametric test of predicted order (described in Sarris and Wilkening 1977).
2. The predicted order is 3-2-1.
3. Replicates were not randomized over the entire 6/7/82 series; all traps tested for a given collecting interval (270, 390, or 510 min) were tested in succession, but replicates of the four trap designs were randomized within these blocks of time.

The predicted order occurred significantly more often than would be expected by chance, for the 510-min collections during series 6/7/82 ($\alpha \leq 0.05$), for the 6/24/82 series ($\alpha \leq 0.01$), for the 8/24/82 series ($\alpha \leq 0.05$), and for all series combined ($\alpha \leq 0.001$). In addition, excluding series 6/7/82, the trends test was significant only for the two longest series (7/22/82 and 8/24/82, where the total duration of trap tests was $\geq$ 6.0 hr, see Table 3.13). Within series 6/7/82, a significant trend also occurred only for the trap tests spanning the longest time interval (2.1 hr for the 510-min collections).

A hypothesis to explain this significant trend in replicate collections is that, within the bead mixtures used to seed the flow, the heavier particles (with relatively large W_c) tend to settle out over time so that a relatively higher proportion of lighter particles (with relatively small W_c) are available to the traps toward the end of a series than toward the beginning. If this is true, then the appropriate value of W_c, for calculations of B_p, would decrease over the time course of each series. Thus, using the same value of W_c (corrected for changes in water temperature) for all trap collecting intervals during the time course of a series would result in underestimated E_r values toward the end of the series. Because W_c spans a range of about one order of magnitude in the 25-μm bead mixture and W_c varies by at least a factor of two in the 46-μm bead mixture, this phenomenon could account for all of the observed variability in the data.

If this hypothesis alone accounts for the variability between replicates (over and above the measurement error), then a positive

correlation should exist between the total elapsed time between replicates of a given trap design and the CV of the mean E_r for that trap. However, no such correlation was evident when these data were plotted for all the traps tested in this study (Figure 3.42). Thus, either this hypothesis is not a plausible explanation, or other sources of variability obscure the expected trends in the data.

The unusually high levels of between-replicate variability also could be associated with the hydrodynamic characteristics of particular trap designs. Evidence that obstacles to the flow that circulates inside a trap (e.g., see Figures 3.35 through 3.41) enhances between-replicate variability in particle collection efficiencies comes from results for the three modified OPC8.5-2.7 trap designs tested during series 8/24/82. The percent CV of the mean E_r was 10.8 for the unmodified trap OPC8.5-2.7. When this trap was screened (trap OPC8.5-2.7S), the precent CV rose to 20.2. The percent CV increased to 25.6 when a honeycomb baffle was inserted to be level with the mouth opening (trap OPC8.5-2.7TB), and to 42.0 when this baffle was pushed down to the bottom of the trap (trap OPC8.5-2.7BB). However, the mean E_r values for these four trap designs were not significantly different (see Figure AII.3, and Appendix II).

The particle concentration in the flume during the trap collections also may have contributed to between-replicate variability in E_r, as evidenced by the significant negative correlation between these terms for replicates of trap OPC8.5-2.7 (see Figure 3.24). A possible mechanism to account for this

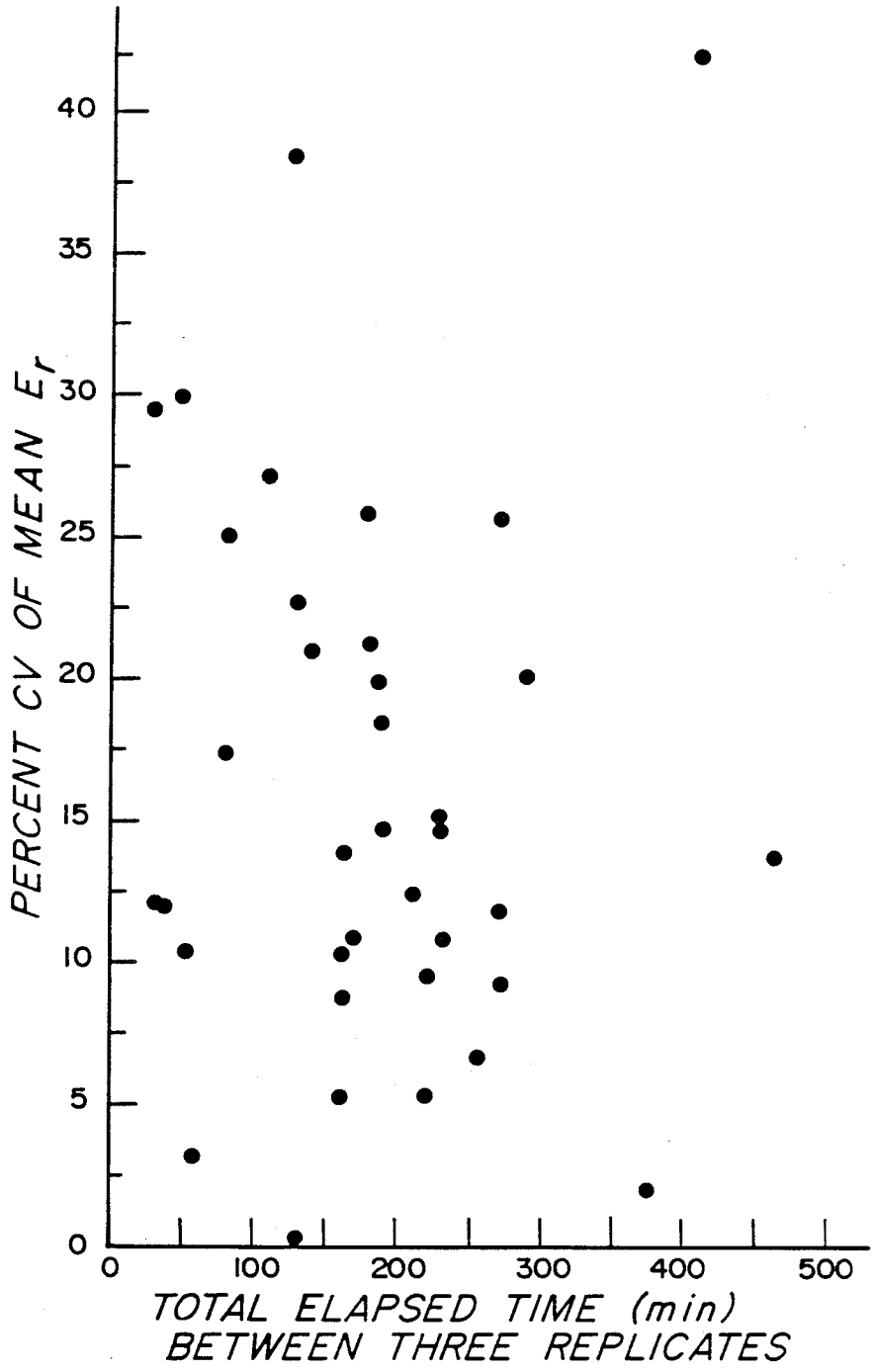


Figure 3.42: Relationship between the total elapsed time between replicate collections by a trap design and the CV of the mean E_r for that trap.

relationship is that, at higher particle concentrations, particle-particle interactions are enhanced resulting in aggregation or disaggregation processes (e.g., see Spielman 1978). Aggregation processes could remove particles from the original bead mixtures, possibly changing, over time, the frequency distribution of bead fall velocities in the flow. In addition, series lasting for longer durations allow more time for aggregation processes to develop and have a significant impact. If the relatively large beads were selectively removed from the flow by aggregation, then the constant W_c (corrected for water temperature) values used in this study would be overestimates toward the end of a series. In this case, if W_c was appropriately corrected throughout a series, the between-replicate variability should decrease. However, if the relatively smaller beads were selectively removed from the flow by aggregation, then the constant W_c (corrected for water temperature) values used in this study would be relative underestimates toward the end of a series. Correcting W_c might then result in even greater reductions in E_r values, toward the end of a series, than are listed in Appendix III. In this case, the decrease in E_r over the time course of a series, for a given trap design, would be a physical reality and not a methodological artifact.

A hypothesized decrease in E_r for some range of decreasing W_c was suggested by the literature and by theoretical arguments in Chapter Two (Section 2.4.3). The differences between series in the E values for trap OPC8.5-2.7 (see Figure 3.22) do not support this hypothesis, unless sonication enhances aggregation. Assuming that

particle aggregation was least likely to occur during series 8/24/82, when 25-μm bead mixtures were sonicated before they were added to the bead tank, then the mean W_c may have been lower for this series than for any other series. The highest E values also occurred during this series. The variability in E values between the other four series may have resulted from variability in the degree of particle aggregation, due to differences in conditions between the series. For example, maximum particle concentrations were much higher during series 6/24/82 and 7/10/82, compared with series 6/7/82 and 7/22/82 (see Table 3.10) and the lowest E values also occurred during the former two series. Because the range in E values during series 7/22/82 (using the 25-μm bead mixture) encompassed the range in E values during series 6/7/82 (using the 46-μm bead mixture) (see Figure 3.22), the higher maximum particle fall velocities in the 46-μm mixture (see Figure 3.16) did not have a detectable effect on E, given the other sources of error in this flume study.

This discussion of some mechanisms which may have produced the between-replicate and between-series variability in particle collection efficiencies is provided to focus attention on conditions that must be carefully controlled, parameters that must be carefully measured and monitored, and hypotheses that require testing in future laboratory studies of particle collectors. Other than the examples given here to support one hypothesized mechanism or another, it is impossible, without further experimentation, to determine which of these mechanisms is primarily responsible for the variability in the data.

In the four relevant published laboratory flume studies that determined particle collection efficiencies of traps (Peck 1972; Tauber 1974; Gardner 1980a; and Hargrave and Burns 1979), results for replicate tests of a given trap design during identical experimental conditions (equivalent to a "series" in the present study) are presented only once. (However, Hargrave and Burns stated that collection efficiency variation between traps was $\leq$ 4 percent when 24 replicates of one trap design were tested simultaneously.) Gardner (1980a) tested two replicates of one trap design (designated as trap "M" in Figure 2.7) during his "Experiment 1" (see Table 3, page 23 of Gardner 1980a). For this case the between-replicate variability in his "trap efficiencies" was 8.5 percent (CV for a mean efficiency of 100 percent.). However, conditions during several of Gardner's nine experiments were sufficiently similar that, at least, the between-experiment variability in trap efficiencies of five trap designs could be estimated. For these trap designs (see Figure 2.7 for trap dimensions corresponding to the letter-designations, used below, for these traps), the mean trap efficiencies ± SD and the percent CV (in parentheses for N number of estimates) were: 95.7 ± 14.7 (15.4, N=3) for trap A, 114.7 ± 22.5 (19.8, N=3) for trap B, 98.3 ± 9.3 (9.4, N=3) for trap C, 541.0 ± 97.7 (18.1, N=3) in the 4.0-4.4 cm/sec flow experiments for trap L, 678.7 ± 302.4 (44.6, N=3) in the 8.9-9.5 cm/sec flow experiments for trap L, and 121.0 ± 36.9 (30.5, N=3) for trap M. Thus, the total range in percent CV for approximately replicate collections by five trap designs was 9.4 to 44.6, with an average percent CV of 22.9.

The similarity in reproducibility between approximately replicate trap tests in Gardner's (1980a) study and in replicate trap tests in the present study (mean CV = 22.9 ± 12.6 percent and 16.1 ± 9.7 percent, respectively) is startling, given the considerable differences in experimental design and in procedures used in the two studies. These results indicate that somewhere between 5 and 35 percent variability in replicate tests of a given trap design is to be expected, thus far, for state-of-the-art flume studies of particle collection efficiencies. Thus, the efficiencies of two trap designs must differ by an average ~ 20 percent to be considered biased collectors, relative to each other.

3.4.5 Hydrodynamical mechanisms responsible for observed trap biases

The quantitative results of this flume study demonstrate that certain trap designs overcollect particles relative to collections by trap OPC8.5-2.7, while other traps are relative undercollectors, in turbulent laboratory flows of ~ 10 cm/sec. While some qualitative observations (e.g., the dye study) and the theoretical arguements presented in Chapter Two allow speculation on the hydrodynamic machanisms responsible for these observed trends, the specific hypotheses presented here remain to be experimentally tested. For the purposes of testing the biological hypothesis central to this dissertation research, it was not necessary to determine the mechanism(s) that created the relative differences in particle collection efficiencies between-trap designs. As long as the inert particles used in the flume and larvae are "seen" as hydrodynamically

similar objects to the flow, then the various trap designs are expected to collect passively falling larvae in the same relative abundances that these traps collected beads in the flume. Such hydrodynamical-similarity was attempted here by using beads having fall velocities within the range of the fall velocities measured for nonswimming larvae. In addition, results of the larval fall velocity measurements indicate that larvae probably are falling like Stokes' particles (see Section 3.4.1). Still, it is fruitful to delineate the possible hydrodynamical mechanisms responsible for trap biases in order to assess the possible role of these physical processes for distributing larvae in nature.

The dye study showed that flow streamlines, centrally-located at approximately the height of the trap mouth, are displaced vertically by the presence of the trap form. The obstruction to the flow causes a local acceleration as the flow veers up over the trap mouth. Pressure drag evidently develops quickly over the trap mouth and turbulent eddies are shed over the opening. Dye entered all traps only at the downstream inside perimeter and exited only at the upstream inside perimeter of the mouth openings. For all traps tested, a single cell of counterclockwise (for flow moving from right to left) of circulating fluid was observed inside the traps. This circulation cell penetrated to the bottom of traps TBC7.4-2.9, TBC14.7-1.6, and the trap similar to OGC8.3-3.0. The depth to which the cell penetrated was not tested for the other trap designs.

The quantitative differences in particle collection efficiencies between traps in the four groups designated in Section 3.3.6 are

summarized below. (1) The small-mouth wide-body trap (OPG8.3-3.0) was an overcollector relative to a cylinder of similar height and mouth diameter (trap OPC8.5-2.7). (2) A relatively small funnel (e.g., in traps OPF8.3-1.9 and OPF8.5-1.9) inserted into the mouth opening of a relatively small-diameter cylinder (trap OPC8.5-1.9) decreased the particle collection efficiency of the cylinder, but probably only if the washings from the funnel surface are not included as part of the sample. (3) A relatively large funnel (e.g., in trap TBF14.7-1.6) inserted into the mouth openings of a relatively large-diameter cylinder (trap TBC14.7-1.6) did not significantly decrease the collection efficiency of the cylinder, whether or not the funnel-washings were included as part of the sample. (4) A relatively small-diameter cylinder with a treaded mouth opening (trap OPC8.5-2.7) may have had significantly higher collection efficiency than a larger-diameter completely straight-sided cylinder (trap TBC14.7-1.6) of the same height, but this was not conclusively demonstrated in this study because the between-replicate variability for trap TBC14.7-1.6 was much lower than the measurement precision for the experiments (see Figure 3.34).

The flow differences between-trap designs that could be ascertained from the dye study are summarized below. The hypotheses which follow, accounting for the quantitative results summarized above, are consistent with these qualitative observations. (1) For the cylindrical traps, TBC1.7-3.0, TBC3.6-3.0, TBC7.4-2.9, TBC14.7-1.6 and TBC14.7-2.9, the diameter of eddies shed over the trap mouth increased with increasing trap mouth diameter (e.g., see Figures 3.35B

and D and 3.36A and B). However, for the small-diameter traps, eddies larger than the mouth diameter were sometimes shed in the lee of the trap opening. (2) The proportional distance (relative to trap height) below the trap mouth at which a centrally-located flow streamline is displaced horizontally (moving sideways, around the trap) and not vertically (moving up over the trap mouth) was greater for the small-mouth wide-body trap (the trap similar to OPG8.3-3.0) than for the cylinder, trap TBC7.4-2.9 (compare Figure 3.35C and D with Figure 3.38C and D). (3) The counterclockwise circulation cell traveled only around the inside of the funnel inserted into trap TBC7.4-2.9 and very little dye flowed through the bottom opening of the funnel (see Figure 3.40B). (4) Turbulent eddies were not shed over the leading edge of the plate surrounding the mouth opening of trap OPP8.3-2.7; the flow approximately paralleled the plate until the flow reached the mouth opening, then eddies were shed over the trap mouth (see Figures 3.41A, B and C). The plate also acted as a barrier, blocking vertically displaced flow below the mouth opening from veering up over the trap (see Figure 3.41D).

Three hypotheses are provided here to explain why the small-mouth wide-body trap (OPG8.3-3.0) relatively overcollected particles compared to a cylinder (trap OPC8.5-2.7) of similar height and mouth diameter. First, particle collections may be a function of the angular velocity (ω) of the circulating cell of fluid inside the trap. At relatively high ω, particles may circulate with the fluid in the eddy for shorter periods of time than at a relatively low ω

(see Section 2.4.2); for the latter case, proportionally more particles would be able to sink out of the eddy and onto the trap bottom. The radius (r) of the eddy, initially shed into the mouth opening, cannot exceed the trap mouth radius. Assume that this eddy (shed at the mouth opening) has a radius of r_1, and an angular velocity of ω_1. Inside a trap, the eddy radius still cannot exceed the trap radius, so in a cylindrical trap (OPC8.5-2.7) the eddy will still be characterized by r_1, and ω_1. However, in trap OPG8.3-3.0, the trap body radius is almost twice the mouth radius so the eddy initially shed into the trap mouth can spread out inside the trap as it continues to circulate as a single cell. Now the eddy inside the trap is characterized by the new dimensions, r_2 and ω_2. For the same eddy moving through a trap, $r_1\omega_1 = r_2\omega_2$. Because $r_2 \simeq 2r_2$, ω_2 of the eddy inside trap OPG8.3-3.0 is about half ω_1 of the eddy inside trap OPC8.5-2.7. Thus, because the eddy characterized by ω_2 takes longer to make one revolution inside the traps, particles may have a greater opportunity to sink out of this eddy than the eddy characterized by ω_1.

Second, because the dye study showed that trap OPG8.3-3.0 causes fluid from a relatively greater distance below the trap mouth (compared to trap TBC7.9-2.9, similar in dimensions to trap OPC8.5-2.7, see Table 3.1) to veer up and travel over the trap opening (rather than being deflected sideways to go around the trap), there may be a greater supply of particles to the mouth opening of trap OPG8.3-3.0 than to the mouth opening of trap OPC8.5-2.7. The fluid displaced by the trap must undergo a local acceleration as it

changes direction. Thus, some particles slightly upstream of the trap, that have fallen below the height of the mouth opening, could be carried up over the trap mouth in this accelerating fluid. The particles could then fall into the trap once the fluid returned to its preacceleration velocity or the particles could be entrained in the eddy shed into the downstream inside perimeter of the mouth opening. This instantaneous local increase in the horizontal flux of particles over the trap mouth would be accompanied by a local decrease in flux in the region of flow slightly upstream of the trap and below the mouth opening which, together, account for the total mass flux within the control volume. However, if the flow accelerates at greater speeds over trap OPG8.3-3.0 than over trap OPC8.5-2.7, then the ω for eddies shed into the mouth of the former trap also would be higher; ω is limited by both the velocity (u) of the flow over the trap mouth and the trap radius, since $u = \omega r$. Only direct measurements or experimental manipulations will determine the trade-offs in particle collections among the relative (compared to trap OPC8.5-2.7) increase in particle flux over trap OPG8.5-3.0, the relatively higher ω at the mouth of trap OPG8.5-3.0 and the potential decrease in ω inside this trap.

Third, the high particle collection efficiencies for trap OPG8.3-3.0 may be an artifact of normalizing collections by the wrong trap diameter. Hargrave and Burns (1979) and Bloesch and Burns (1980) have suggested that the effective trap mouth surface area for small-mouth wide-body traps is actually the body diameter, as long as particle concentrations outside the trap and inside the trap quickly

reach a steady state. They suggested that, if the trap mouth is well flushed with fluid from the outside, then the particles are actually falling through a surface area characterized by the body diameter and not the mouth diameter. However, if E_r values were calculated based on the body diameters of all the small-mouth wide-body traps tested in this study (see Table 3.14 for traps OPG8.3-3.0, OPG8.3-3.0S, and OPG8.5-3.6), then the traps are relative undercollectors compared to cylinders of similar height and mouth diameter. Thus, this hypothesis alone cannot account for differences in relative collections by traps OPC8.5-2.7 and OPG8.3-3.0.

Two hydrodynamical processes may contribute to the relative undercollection of particles by the cylindrical trap with a plate surrounding the mouth opening (trap OPP8.3-2.7), compared to the same cylinder without the plate (trap OPC8.5-2.7). First, the plate surface imparts a larger frictional drag to the oncoming flow. As evidenced in the dye study, the flow slows down as it moves across the plate and the separation zone does not occur until the flow passes over the mouth opening, where eddies are then shed into the trap. Particles can fall out of the low flow region and accumulate on the plate surface; the author actually observed beads piling up on the plate during flume tests of these traps (see Section 3.3.6). Thus, fewer particles would be left in the flow supplied to the mouth of trap OPP8.3-2.7 than to the mouth of trap OPC8.5-2.7. Second, the plate acts as a horizontal barrier to the flow, slightly upstream of and below the trap mouth, that would be deflected up over the mouth opening of a cylinder. Thus, a supply of particles from below the

TABLE 3.14

Particle Collection Efficiencies of Noncylindrical Traps Using an Inside Diameter, Other than at the Mouth, in Calculations

Trap design[1] (series)	Inside diameter at mouth (cm)	mean E_r ± SD () = N	Inside diameter below mouth[2] (cm)	mean E_r ± SD () = N
OPG8.3-3.0 (7/10/82)	8.3	206.7 ± 19.6 (3)	15.2	61.7 ± 5.9 (3)
(7/22/82)	8.3	185.6 ± 37.2 (3)	15.2	55.4 ± 11.1 (3)
(8/24/82)	8.3	228.4 ± 20.1 (3)	15.2	68.2 ± 6.0 (3)
OPG8.3-3.0S (8/24/82)	8.3	240.0 ± 7.6 (2)	15.2	71.6 ± 2.2 (2)
OPGC8.5-3.6 (8/24/82)	15.2	233.3 ± 24.2 (3)	8.3	73.0 ± 7.6 (3)
OPF8.5-1.9 (6/7/82)[3]	8.5	26.6 ± 7.9 (3)	1.1	1288 ± 380 (3)
OPF8.3-1.9 (8/24/82)[3]	8.3	34.4 ± 10.1 (3)	1.1	2332 ± 687 (3)
(8/24/82)[4]	8.3	81.6 ± 9.9 (3)	1.1	4532 ± 553 (3)
OPF14.1-3.6 (7/22/82)	14.1	75.6 ± 13.9 (3)	8.3	218.6 ± 40.1 (3)

TABLE 3.14 (cont. - 2)

Trap design[1] (series)	Inside diameter at mouth (cm)	mean E_r ± SD () = N	Inside diameter below mouth[2] (cm)	mean E_r ± SD () = N
TBF14.7-1.6 (8/24/82)[3]	14.7	80.6 ± 12.2 (3)	7.8	285.8 ± 43.9 (3)
(8/24/82)[4]	14.7	88.1 ± 12.9 (3)	7.8	312.5 ± 45.7 (3)

1. Traps listed by codes in Table 3.1.
2. For trap OPG8.3-3.0, this is the diameter of the body beginning ≃ 3-cm below the mouth and for all other traps, this is the inside diameter at the bottom of the funnel.
3. Without funnel-washings.
4. Including funnel-washings.

mouth opening (see second hypothesis for trap OPG8.3-3.0) is eliminated for the plate-trap design.

The funnel traps, OPF8.5-1.9 and OPF8.3-1.9, may be considered undercollectors relative to the cylinders, OPC8.5-1.0 and OPC8.5-1.9, only if the washings from the sides of the funnels are not considered part of the trap collections (see Figure 3.32). This situation holds for field deployments of funnel traps used in the present study because the funnels were removed from the traps before they were capped underwater (see Section 4.2.1). Clearly, particle build-up on the funnel surface is responsible for the relative undercollections by these trap designs. The dye study showed that a counterclockwise (for flow moving from right to left) eddy circulated around the funnel; the frictional drag of the funnel surface may have sufficiently slowed down the flow so that particles falling out of the flow onto the funnel surface could not be resuspended. Evidently the funnel was not steep enough and/or smooth and nonsticky enough for some of these particles to then roll down into the bottom funnel opening. However, surprisingly more particles passed through the funnel openings than would be predicted if the bottom funnel diameter (rather than the mouth diameter) was used in calculations of the collection surface area of this trap design (see Table 3.14).

It is curious that the funnel traps, OPF8.5-1.9 and OPF8.3-1.9, undercollected particles relative to cylinders of similar height and mouth diameter, while the funnel trap, TBF14.7-1.6S, did not significantly undercollect particles (when funnel-washings were or were not included in the analyses) relative to either trap

TBC14.7-1.6 or trap OPC8.5-2.7. Because the funnel traps (TBF14.7-1.6) were screened and the cylinders (TBC14.7-1.6) were not, collections by those two trap designs are not precisely comparable. However, collections by screened versions of trap TBC14.7-1.6 probably would not differ significantly from the collections by unscreened traps. Screening trap OPC8.5-2.7 during series 7/10/82 and 8/24/82 increased the variability in replicate collections and slightly increased the mean E_r values compared to unscreened traps during these series (see Figure 3.27), but the differences were not statistically significant (Mann-Whitney U tests, the H_0 could not be rejected at $\alpha \leq 0.05$); screened and unscreened collections by trap OPG8.3-3.0 during series 8/24/82 overlapped completely (see Figure 3.27). Because the diameter at the bottom of the funnel in trap TBF14.7-1.6 is relatively large compared to the mouth diameter of this trap (the bottom funnel diameter is 54 percent of the mouth diameter of trap TBF14.7-1.6, but only 13 percent of the mouth diameter of traps OPF8.5-1.9 and OPF8.3-1.9), maybe the eddy shed into the mouth opening does enter through the bottom funnel opening and circulate in the main body of the trap. (Unfortunately, trap TBF14.7-1.6 was not observed in the dye study.) However, it is difficult to envision the eddy circulating back up and leaving the trap at the upstream perimeter of the bottom funnel opening, as the circulating cells were able to leave the upstream perimeters of the cylindrical mouth openings. Once the eddy got through the bottom of the funnel it would probably increase in diameter to circulate through the whole body of the trap (as in trap OPG8.3-3.0). Thus,

these eddies may be "caught" below the funnel inside trap TBF14.7-1.6. Trap TBF14.7-1.6 then would be expected to have trap collection efficiencies more similar to a small-mouth wide-body trap (using the diameter at the bottom of the funnel for calculations of the collection surface area) than to a cylinder (using the diameter at the top of the funnel for calculations of the collection surface area). Calculations of particle collection efficiencies of trap TBF14.7-1.6, using the surface area at the bottom of the funnel, support this hypothesis (Table 3.14). However, the same calculations for trap OPF14.1-1.6 (Table 3.14) also yield relative particle collection efficiencies more similar to trap OPG8.3-3.0 than to trap OPC8.5-2.7. Because trap OPF14.1-1.6 is cylindrical from the bottom of the funnel opening to the trap bottom, some other explanation is required to explain these relative overcollections.

From this discussion of some of the mechanisms responsible for the biased collections observed in this study, three points are emphasized. (1) The hydrodynamic process(es) underlying particle collections by the traps specifies the physical dimension for scaling collections between trap designs. The trap mouth diameter was used for all calculations here because of the biological hypotheses to be tested in this study: if larvae are actively chosing a settlement site, the trap mouth openings would be surfaces, of a given area, into which larvae could swim. Changing this scaling dimension (e.g., from the top funnel diameter to the bottom funnel diameter), can, for example, turn a relative undercollector into a relative overcollector. Thus, the physical processes controlling particle trappings must be

understood before traps can be accurately categorized as biased or unbiased collectors. (2) While intuition and understanding of some of the hydrodynamical processes yields many hypotheses to explain biased collections, clearly measurements and experiments are needed to determine the exact effects and the relative importance of the mechanisms outlined here. (3) It is not yet possible to make accurate flux estimates using any kind of trap. Even comparisons between collections by the same trap design deployed under different physical conditions may be unjustified if collection efficiency is a function of trap Reynolds number (e.g., see Appendix II), particle fall velocity, and particle concentration.

3.5 Summary

The nonswimming fall velocities of planktonic larvae of several polychaete species (Eteone longa, Streblospic benedicti, and other spionid species) were measured in the laboratory. The larvae were anesthetized and then introduced into a temperature-controlled column of seawater, where fall velocity measurements were made. Calibrations of the techniques using spheres indicated that the imprecision in the fall velocity measurements was about 10 percent. For larvae ranging from 300 to 1400 μm in narcotized length, fall velocities (normalized for 30 ppt salinity, 20.4°C seawater) ranged from 0.0129 to 0.374 cm/sec. Fall velocity was positively correlated with narcotized length. The larval fall velocities are equivalent to the theoretical fall velocities (normalized to the same seawater conditions) of spherical quartz particles ranging from 16 to 70 μm in

diameter. Thus, the nonswimming polychaete larvae tested fall primarily like silt particles (quartz particles ranging from 3.9 to 62.5 μm in diameter) in the ocean. Based on the larval fall velocity measurements, two mixtures of spherical glass beads were selected to seed the flume flow: theoretical fall velocities (in 24°C freshwater) ranged from 0.014 to 0.32 cm/sec for ~ 97 percent of the 25-μm bead mixture and theoretical fall velocities (in 24°C freshwater) ranged from 0.081 to 0.42 cm/sec for ~ 94 percent of the 46-μm bead mixture.

The particle collection efficiencies of sixteen different trap geometries, as well as screened and baffled versions of some of these traps, were tested in a freshwater laboratory flume during five series of experiments. The flow was continuously seeded with the bead mixtures indicated above and the flow speed was about 10 cm/sec, with the range of flow speeds measured 1.0-m above the bottom at the field study site (see Section 4.3.3). Flume experiments were carefully designed to achieve dynamic and geometric similarity to field conditions.

Only relative particle collection efficiencies were calculated for the traps tested in this study; all collection efficiencies were normalized by the mean particle collection efficiency of a cylindrical trap that was tested during each series. This trap design was also used in nearly all of the field experiments. Calculated total measurement error for the techniques used in this study indicated that an average of ~ 10 percent imprecision could be expected for replicate tests of the same trap design. The average

measured between-replicate variability was ~ 16 percent, but varied between 0.1 and 42 percent. Thus, trap designs were considered biased collectors, with respect to each other, only if their particle collection efficiencies differed by 20 percent, or by the combined CV for the two trap designs, whichever value was largest.

Based on results of the flume study, four groups of traps were selected for deployment in the field. Specific a priori hypotheses were stated regarding the rank order of particle collections by the trap designs within each group. Collections of larvae by the traps within each group can then be compared to the a priori predictions, to test the H_0 that larvae and passive particles are similarly collected by the traps.

Several hydrodynamic hypotheses were presented to explain the biased trapping of particles by some of the trap designs tested in this study. The hypotheses are based on a qualitative dye study of the flow near and within the mouths of several trap designs, the quantitative results presented in this chapter, and the theoretical analysis presented in Chapter Two. The hypotheses remain to be experimentally tested.

The results of this flume study suggest that the collection characteristics of traps must be researched in much more detail before reliable measurements of particulate flux can be made with any trap design.

4. FIELD EXPERIMENTS TO TEST THE HYPOTHESIS THAT LARVAE SINK LIKE PASSIVE PARTICLES THROUGH NEAR-BOTTOM WATERS

4.1 Introduction

All field experiments designed to test the hypothesis that larvae and inert particles, with fall velocities similar to larvae, act similarly in turbulent flows near the seabed are discussed in this chapter. During the summer of 1980, prior to the theoretical analysis of trap biases (Chapter Two) or the laboratory measurements (Chapter Three), a variety of trap designs were deployed at the study site (see Section 4.1.2) as a pilot study of larval settlement in the area. The predicted order for collections of larvae by these trap designs was based on the results of Gardner's (1980a) laboratory calibration of sediment traps. However, following the 1980 experiments, a critical review of the sediment trap literature revealed disturbing ambiguities regarding the measured collection efficiencies of particular trap designs both within- and between-studies (e.g., that collection efficiency decreased with increasing trap Reynolds number in some studies and not in others, see Section 2.3); these findings stimulated the theoretical analysis of trap biases. Results of the theoretical analysis indicated that biased trap collections may be flow-regime and particle-type dependent (see hypotheses presented in Section 2.4) and, thus, Gardner's (1980a) results were not sufficient for developing accurate a priori hypotheses regarding the collection of larvae (a particular class of particles) at the chosen study site (a particular flow regime) for

traps deployed during the 1980 experiments. The flume study to determine trap biases for the flow regime and particles of interest in the present study preceeded the second set of field experiments conducted during the summer of 1982. Thus, while all trap designs discussed in this chapter were calibrated in a flume for the particles and the flow regime in question, the rank order of collections by these traps supplied a priori hypotheses for experiments during the summer of 1982, but only a posteriori hypotheses for experiments during the summer of 1980.

4.1.1 Choice of traps for field deployment: considerations of larval biology

For the field experiments conducted in this study it is important to distinguish between "random" collections, "passive" collections, and "biological" collections of larvae by traps. It has been suggested (e.g., see review by Thorson 1957) that an alternative hypothesis to active habitat selection by larvae is that larvae are deposited "at random" on the seabed. Random deposition explicitly states that there is an equal probability that individual larvae will fall onto any given location of the bed. The random deposition hypothesis has been suggested as a null hypothesis against which biological effects can be ested; that is, the depositional sites for biological particles (larvae) are expected to be similar to the settlement sites for non-biological particles (e.g., sediments) only if biological processes have a negligible effect on the deposition of larvae. However, it is emphasized here that random deposition is synonomous with "passive" deposition only for a well-mixed (i.e., homogeneous) suspension of larvae falling through still water.

In moving water, for an infinite water mass with a uniform particle supply distributed homogeneously in the water column and with a steady and nonvarying physical regime, the initial distribution of particles on the seabed would be random. However, for temporally and/or spatially varying flow regimes, particle abundances, and particle distributions in the water column, the particles would not fall at random onto all regions of the seabed. In this case, the sites for initial settlement of particles are determined by the hydrodynamical processes and the particle characteristics. Thus, for the physical regime of interest in this and most other ocean studies, random larval deposition is not the appropriate null hypothesis for testing biological effects in moving water. If biological processes have a negligible effect on larval deposition in flows, then larvae should initially reach the seafloor at locations where inert particles, with hydrodynamic characteristics similar to larvae (e.g., fall velocities, see Chapter Two) initially settle. This is the "passive deposition" hypothesis; it is a more general null hypothesis than the random deposition hypothesis because the passive deposition hypothesis is appropriate for both still and moving fluid and the random deposition hypothesis is appropriate only for still water and for unrealistic circumstances in moving water. Larval settlement is considered "biological" when active behaviors or physiological responses of the larvae determine their initial depositional sites on the bed. However, a problem arises if biological processes cause larvae to settle in patterns that correspond to those predicted for passive particle deposition; this

problem is discussed below.

Collections of larvae by traps also can be classified as random, passive or biological, according to the definitions given above. However, the hypothesis in these field experiments is that larvae are passively collected by traps, because all experiments were conducted in flows. The mouth opening of a trap presents a surface area through which larvae can fall. If larvae fall like passive particles, then the relative flux of larvae (number of individuals per unit area per unit time) through the mouths of the various trap designs should be similar to the relative flux of particles into these trap designs, as determined in the flume study (Chapter Three). In this case, the null hypothesis (H_0) of no difference in collections of larvae and of passive particles by traps would not be falsified. If hydrodynamic processes do not determine the collections of larvae by traps, then the relative flux of larvae into the traps would significantly differ from the relative flux of particles into traps and the H_0 would be falsified. In addition, if the abundances of larvae in the traps does not differ significantly from the abundances predicted for <u>random</u> collections, then the passive collection null hypothesis is also falsified. It is again emphasized that, in flows, passive particles are not collected in traps at random, but in the relative abundances determined by hydrodynamical processes.

If the H_0 cannot be falsified, that is, if relative differences in collections of larvae and of particles between trap designs is not significantly different, the possibility still exists

that the collections resulted from biological and not physical processes, or that a combination of these and other processes was involved. It is the nature of null hypothesis testing that accepting an H_0 is not explicit evidence that the process tested is, in fact, operating while falsification of the H_0 is explicit evidence that, at a given significance level, the process tested is not operating. Thus, the explicit result of falsifying the H_0 tested in the present study is that passive physical processes do not determine sites for initial settlement of larvae onto the seabed. If the H_0 is not falsified, then it is likely that passive physical processes determine initial patterns of larval settlement, but alternative hypotheses also must be considered. In fact, further null hypothesis testing would be required to determine the precise role of hydrodynamical processes in larval settlement.

Although 12 trap designs (plus various screened and baffled versions of these traps) were deployed during 1980 and five trap designs were deployed during 1982, results for only eight of these designs (the five deployed in 1982 and three other designs deployed in 1980) are reported here. These trap designs are presented as Groups A through D in Chapter Three (Section 3.3.6). These designs were selected based on results of the flume study (see Section 3.3.6) and on considerations of larval biology, discussed later in this section.

To adequately test the null hypothesis of passive collections of larvae by traps against biological alternative hypotheses, it is important to design field experiments so that larvae are allowed to

behave and react normally. For example, many larvae actively swim, they have phototactic or geotactic behaviors, and/or they can actively choose between certain sediment treatments in the laboratory (this literature is reviewed in Chapter One). This dissertation research does not question whether or not larvae also behave and react in the field; this research questions the extent to which these behaviors or responses determine initial settlement sites for larvae on the seabed during natural field flows.

Clearly, traps raised above the seafloor do not mimic bottom sediments; in fact, mimicking conditions on the seabed by using traps was not the intent of these experimental manipulations. No doubt, trap environments constitute unique hydrodynamical, biological, and perhaps even chemical environments (but see Section 4.2 for a description of the precautions taken in this study to limit biological processes and chemical reactions inside traps) for larvae. However, just as rippled areas of the seafloor dominated by sands and areas dominated by smooth muds are formed and maintained, at least in part, by hydrodynamical processes, sediment collections by different trap designs are also hydrodynamically determined. Again, no attempt is made here to directly link hydrodynamical processes associated with a particular trap design to hydrodynamical processes occurring in a particular sedimentary environment in the field. The important point is that differential sediment collections by various trap designs result from trap-induced changes to the local flow regime (see Section 2.4). Thus, if larvae are collected by traps in the same relative abundances that passive particles are

collected by traps, then hydrodynamical processes are probably determining the collection of larvae in traps. This result would strongly suggest that hydrodynamical processes also may determine initial depositional sites for larvae on the seabed. However, passive larval deposition on the seafloor and the spatial scales for which this occurs would have to be experimentally determined.

The four groups of traps (a total of eight trap designs, see Figures 3.26, 3.29, 3.31 and 3.33; but see also Table 4.2 and Figure 4.10 for the slight modifications to the Group C traps deployed in the field) tested in the flume and deployed in the field were selected for the following reasons. (1) All traps have mouth openings that are large (8 to 15 cm in diameter) compared to the size of larvae (100- to 500-μm long). The biological consideration here was that larvae may behave differently near walls and walls are uncommon in soft-sediment environments. Larvae would not be close to the wall for a substantial portion of the trap mouth area as long as traps have relatively large mouth openings. However, whether or not larvae do perceive or react to walls is unknown so the required distance from the wall, for which the wall's presence would no longer be detected by a larva, is also unknown. (2) The trap designs within each of the Groups A, B and C have similar mouth diameters. Because the traps within each of these groups had relatively different particle collection efficiencies during the flume experiments, if larval settlement into these traps is random these mouth openings would be expected to collect similar numbers of larvae. (3) The trap designs within each of the Groups A, C and D all have similar heights;

thus, larvae would have a similar vertical distance to swim in or out of each of these trap designs. (4) From direct observations (using dye) of flow through these traps (see Section 3.3.7), all trap designs except one (the trap similar to OPF8.5-1.9) were well-flushed with water. Thus, the seawater environment (e.g., the seawater chemistry) in the traps was expected to be similar to the natural seawater environment outside the traps. Effects on the seawater environment (and, perhaps, the chemical nature of the sediments) inside funnel traps (such as trap OPF8.5-1.9) due to the somewhat limited water flow through the body of this trap (e.g., see Figure 3.40) are unknown. However, over a field collection interval of 11 days (the maximum length of a field experiment reported here), anoxic conditions were not apparent inside traps of this design (as determined visually, by inspection of the organisms, and from smelling sediments).

4.1.2 The field study site

The field study site is located in Buzzards Bay, MA (Figure 4.1) at Sanders' et al.'s (1980) "Station 35" (41°37.8'N, 70°40,5'W). Species composition and abundance at the study site has been previously documented at monthly intervals over a two-year period, from September 1969 through August 1971 (Sanders et al., 1980), providing baseline data for the present study.

Station 35 is located in about 15 m of water (see Figure 4.1) and the bottom is composed primarily of medium, "moderately well to poorly sorted" sandy (250-500 μm) sediments (Sanders et al., 1980). Throughout the year the sediment composition was 0.5-6.7 percent

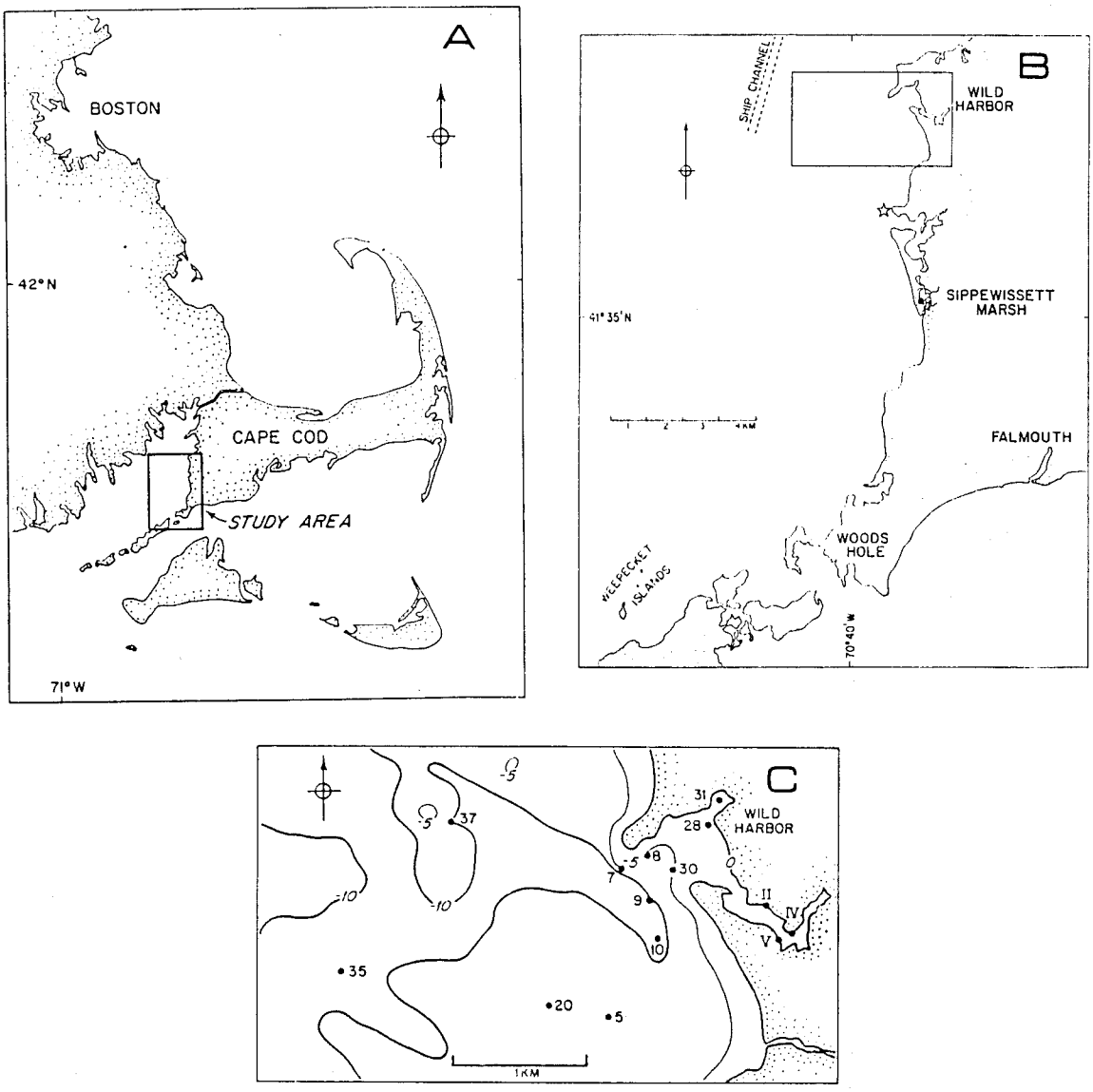


Figure 4.1: Map of the study site showing the location of Buzzards Bay on Cape Cod (A), the location of Sanders' et al.'s (1980) study area in Buzzards Bay (B), and the exact location of Station 35 (C). The maps are reprinted from Sanders et al. (1980).

gravel, 59-90 percent sand, and 10-37 percent mud during the study of Sanders et al. (1980).

A brief summary of results from Dr. Bradford Butman's (U.S. Geological Survey, Woods Hole, MA) study of the physical oceanography at Station 35, conducted concurrently with the present study, is presented later (Section 4.3.3). These are the first continuous measurements of near-bottom currents and other physical parameters (see Section 4.2.4) made in Buzzards Bay. A general description of the physical oceanography in the Bay from studies done prior to Butman's is given here.

Previous descriptions of the physical oceanography of Buzzards Bay have presumed that the currents were primarily tidal (e.g., Redfield 1953), but few measurements have actually been made. Because the main axis of the Bay is oriented northeast/southwest, tidal currents generally are oriented along this axis. However, there is a slight tendency for a counterclockwise gyre in surface current circulation in Buzzards Bay; surface tidal currents are generally weak, rarely exceeding 50 cm/sec (Eldridge 1983) and are slightly stronger and of longer duration during the flood than during the ebb tide.

Buzzards Bay is shallower on the north and northwest shores than along the eastern and southern portions of the Bay. As a result, during the summer, water along the northwest side of the Bay is warmer. The entire Bay is generally vertically stratified during the summer because of surface heating. Along the southern and southwestern portion relatively cold water persists at depth. This

northwest/southeast Bay temperature gradient may result in density-driven circulation in the Bay (W.D. Grant, personal communication). During the winter the water column in most parts of Buzzards Bay is well-mixed.

During the summer, the prevailing winds are from the southwest as a result of the Bermuda high pressure system lying to the southeast of the Cape. Winds are strongest in the afternoon, due to local seabreezes added to the prevailing southwesterly winds. At Station 35, winds from the southwest experience the longest fetch (see Figure 4.1) so local seas at the study site can reach heights of 1-1.2 m in 2-3 hours. However, in non-storm conditions, locally generated wind waves in the Bay are fetch-limited to approximately 4 seconds and rarely penetrate to the bottom at Mid-Bay. The low-pressure systems associated with winter storms track southwest/northeast. The lows usually move offshore to the south of the Cape so that north or northeastern storm winds prevail. These storms generate significant local seas which penetrate to the bottom over the entire Bay (W.D. Grant, personal communication). Occassionally, southwestern storm winds occur and cause the largest waves in the Bay.

Available Buzzards Bay temperature and salinity measurements indicate that salinities range from about 29 to 32 ppt and water temperatures range from below zero to at least 23°C (L.K. Rosenfeld, presonal communication). Salinity drops slightly in the spring and is highest during the fall. Water temperatures are at a minimum during February and at a maximum during July and August.

4.2 Materials and Methods

4.2.1 Bottom-moored traps

All field experiments were conducted by SCUBA divers. Of the materials available, those considered to be the most chemically inert in seawater (e.g., plastic, stainless steel, resin, waterproof epoxy, ethylene chloride glue and silicone sealant) were chosen for use in the field. In addition, for the 1982 experiments, all traps were soaked in running seawater for at least 24 hr prior to deployments. Larvae may be attracted to or repelled by particular chemical substances and these precautions were taken to limit such biological effects.

The traps in Groups A through D (diagramed in Figures 3.26, 3.29, 3.31 and 3.33, but see also Table 4.2 and Figure 4.10 for the Group C-like traps used in the field) were placed in "baskets" on PVC posts (1.9-mm diameter) as in the flume experiments (see Figures 3.4 and 4.2). For a distance of ~ 60 cm from the bottom of the posts, "earth anchors" (~ 1-cm diameter, 76-cm tall) were hose-clamped to the posts. Earth anchors are galvanized rods with an eye at the top and a 10-cm diameter screw-like plate at the bottom. The earth anchors (with the attached posts) were screwed into the sediment approximately 70 cm so that just the eye of the anchor protruded above the sediment surface (see Figure 4.2). For deployments during the summer of 1980, galvanized earth anchors were used in the field. Some of these anchors rusted during the course of the experiments so all earth anchors were painted with resin prior to deployments in 1982.

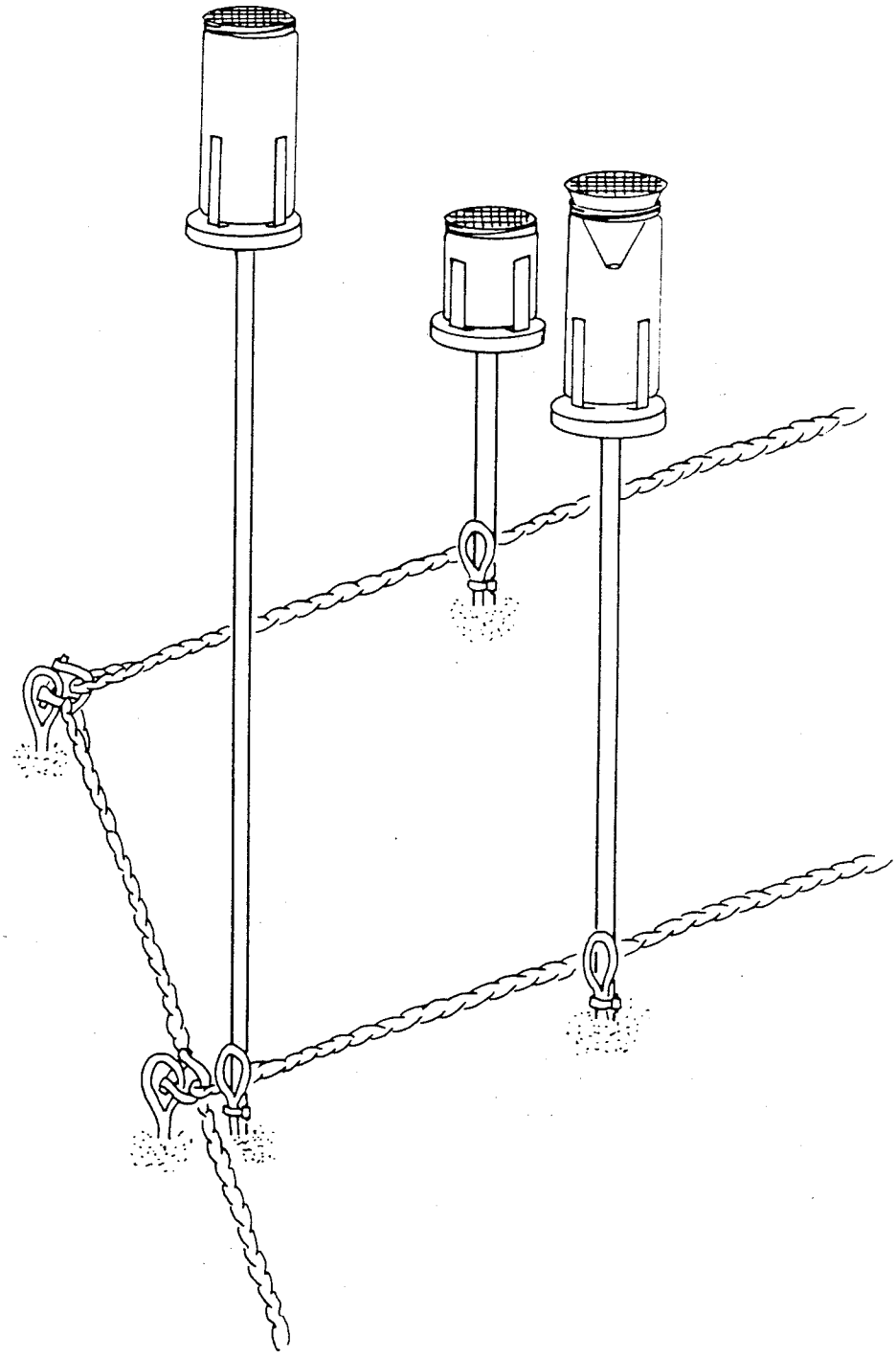


Figure 4.2: Diagram of the Group C-like trap designs on the three post heights used in the 1980 experiments. Also shown are the floating polypropylene transect lines used to mark the positions of the traps.

For the 1980 deployments, posts of three different heights were used; when posts were in place in the field, the heights above the bottom at the top of the posts were 42 ± 6 cm (range = 35 to 61 cm for N = 15 posts), 99 ± 3 cm (range = 95 to 105 cm for N = 9 posts), and 161 ± 3 cm (range = 157 to 166 cm for N = 9 posts). Three posts of each height were arranged, in random order, along each of three approximately parallel (to ± 5°) transects (i.e., there were nine posts per transect); a fourth transect contained six of only the shortest size (42 cm) posts (see Figure 4.3 for locations of posts along transects). The transects were specifically oriented northeast/southwest to parallel the predominant direction of tidal currents (see Section 4.1.2). The parallel transects were about 6-m apart and adjacent traps along a transect were ~ 3.3-m apart (see Figure 4.3). Thus, adjacent traps were separated by about 80 trap radii (for the Group C-like traps, see Figure 4.10) during the 1980 experiments.

For the 1982 deployments, only one post height (the top of the posts were 94 ± 1-cm above the sediment surface) and two different transect arrangements were used at the study site. The first transect arrangement (Figure 4.4A) consisted of two perpendicular lines forming a right (90°) angle, one running northeast/southwest (~ 60° magnetic) and the other running north-northeast/south-southwest (~ 330° magnetic). Four posts were placed ~ 3.3-m apart along each line. After several experiments, this first transect arrangement was revised. The second transect arrangement (Figure 4.4B) consisted of three approximately parallel (to ± 2°) lines, all oriented northeast/southwest (as in the 1980 experiments). Two of the adjacent lines

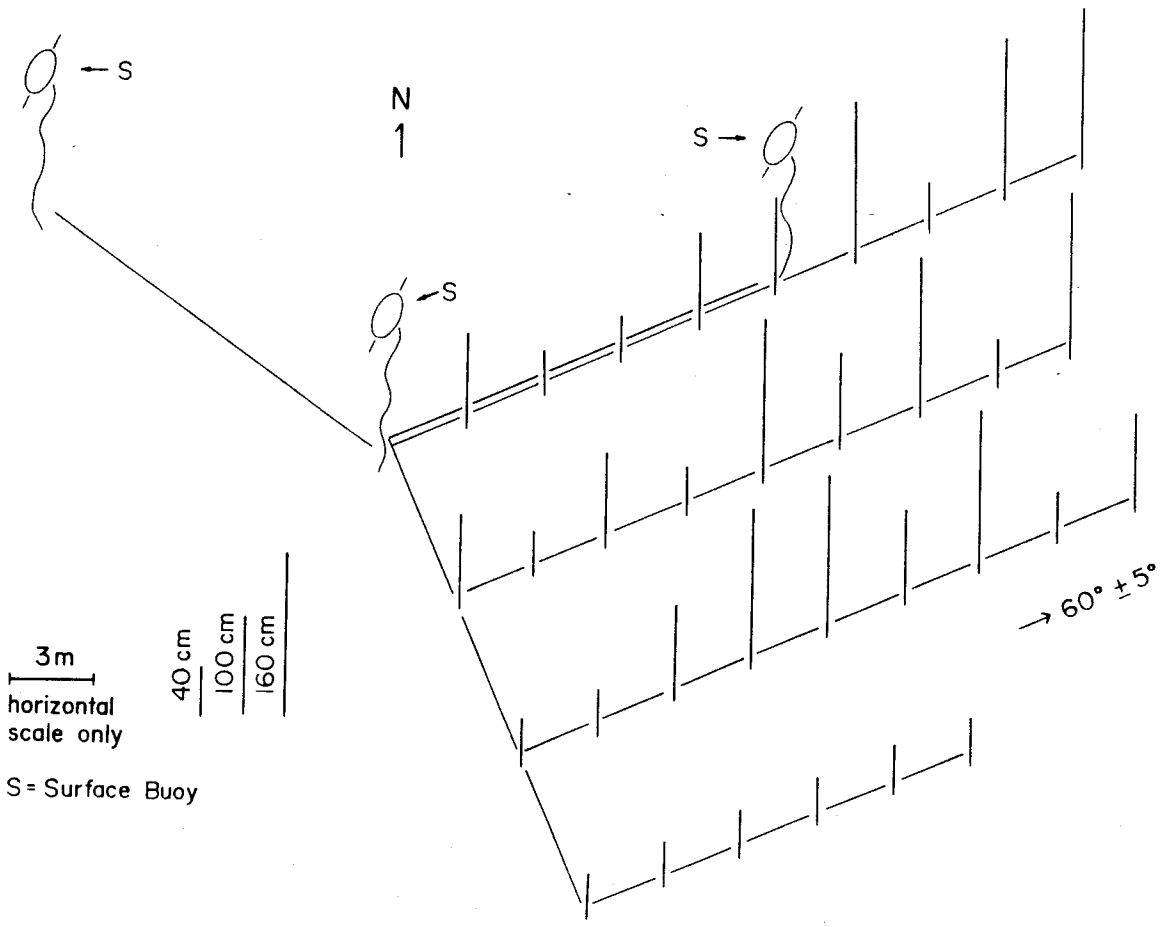


Figure 4.3: Diagram showing the locations, on the bottom at Station 35, of the four approximately parallel transect lines for experiments during the summer of 1980. Also shown are the randomly determined locations of the three post heights (shown, to scale, as vertical bars) along three of the transects. The fourth transect contained only the shortest posts. Three buoys, forming a triangle, marked the station to insure station relocation. Note that the vertical and horizontal scales are different in this diagram.

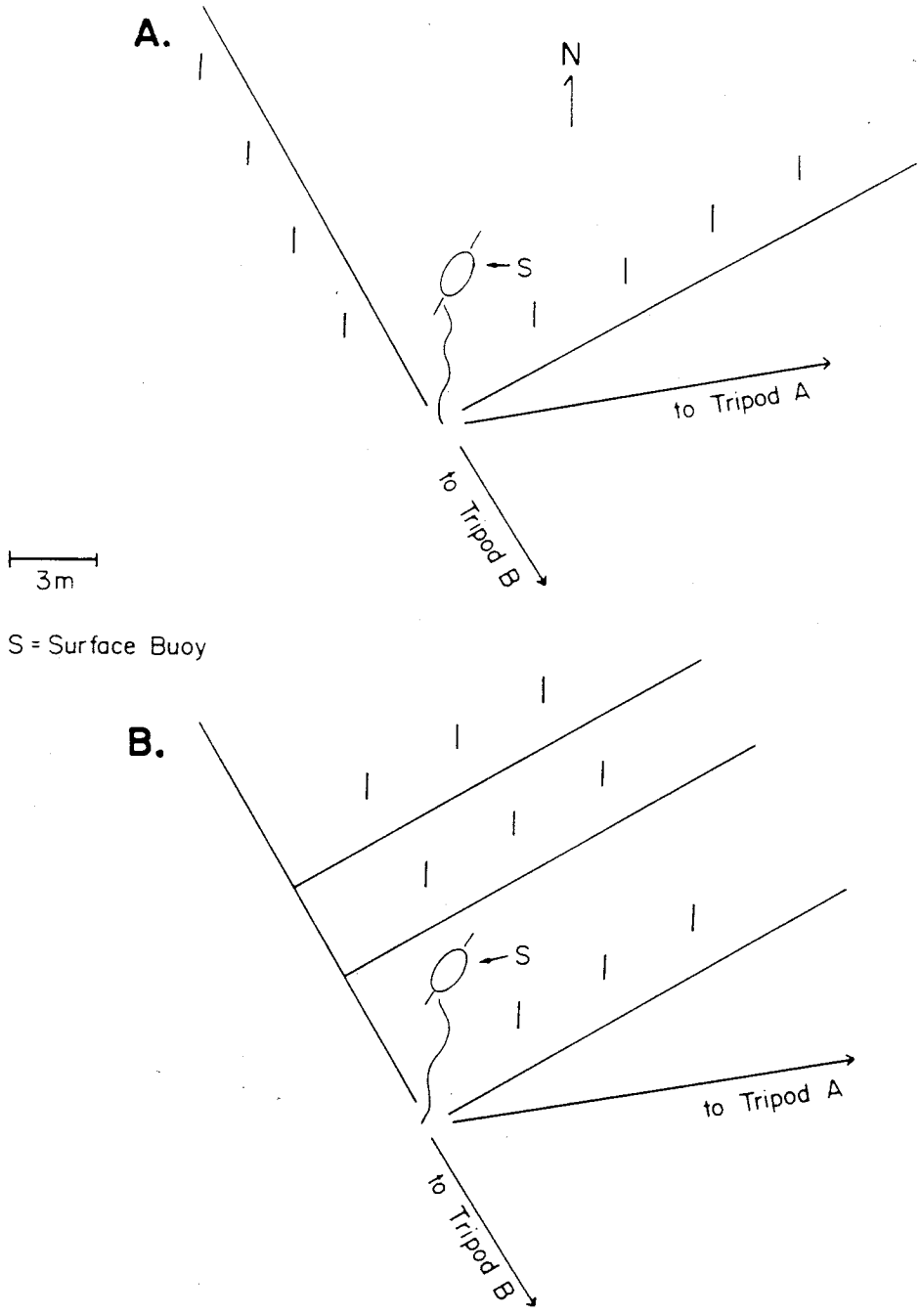


Figure 4.4: Diagram showing the locations, on the bottom at Station 35, of the two transect arrangements (A and B) used during the summer of 1982. The posts are drawn, to scale, as vertical bars on the Figure. The triangular buoy arrangement during this summer is drawn, to scale, in Figure 4.5.

were ~ 5-m apart and the other two adjacent lines were ~ 3.3-m apart (see Figure 4.4B). Three posts were placed along each transect, the adjacent traps separated by ~ 3.3 m. Thus, all adjacent traps during the 1982 experiments were separated by at least 45 trap radii (using the largest trap diameter for the Group A, B and D traps, see Figures 3.26, 3.29 and 3.33).

The polypropylene transect lines were not drawn tight against the seabed but were attached to earth anchors and allowed to float ~ 5-cm above the bottom (see Figure 4.2) to limit flow disturbances to surface sediments. The posts along each transect were screwed into the sediment at distances of ~ 140-cm from the transect line (e.g., see Figures 4.2 and 4.4). The transect lines were necessary so divers could locate the posts on the bottom; visibility at the study site was usually about one meter. Divers also used the lines to pull themselves along the bottom to minimize disturbances to bottom sediments.

The location of the 1980 transects relative to the 1982 transects is shown in Figure 4.5. The positions of the two bottom-tripod systems, deployed during the 1982 experiments, are also shown in this figure. Measurements using these tripods are described later (Section 4.2.5). All experiments were located within approximately an 80-m by 40-m area. Previous studies of sediments in the vicinity of Station 35 indicate that the sediment type characterizing this station covers an area of about 500 m by 500 m (Hough 1940; Moore 1963; Sanders et al., 1980). Thus, in this study, all experiments were conducted within the same general sedimentary environment.

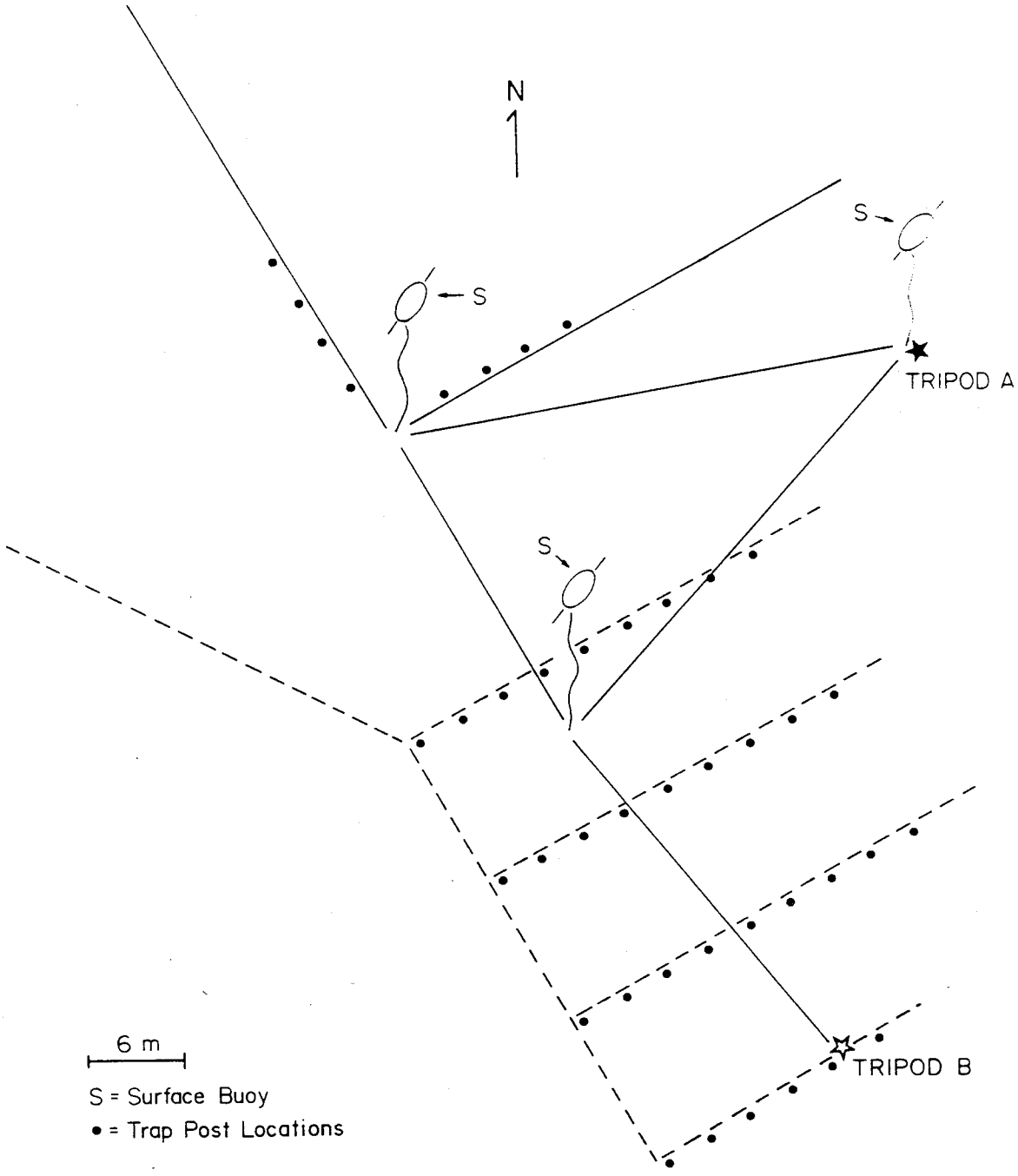


Figure 4.5: Diagram showing the locations of the 1980 transects (dashed lines) and the first transect arrangement (see Figure 4.4A) used in 1982 (solid lines), relative to each other. Also shown (as stars on the Figure) are the locations of the two bottom-moored tripod systems deployed during 1982.

Traps of one design were placed along each of the three long transects (so three trap designs, each at three heights above the bottom, could be tested concurrently) during the 1980 experiments (see Figure 4.3). Specific trap design locations along each transect line were randomized. Only two trap designs were tested concurrently on the right-angle transects (see Figure 4.4A) in 1982. Two traps of each design were placed along each transect in orders determined by a random number table. Three trap designs were tested on the three parallel transects in 1982 (see Figure 4.4B). The placement of each replicate of the three designs was, again, determined by a random number table.

All traps were screened with fine-filament plastic mesh (described in footnote 11 to Table 3.10, see also Figure 4.2). For the 1980 experiments, uncapped traps were carried to the bottom by divers and then each trap was shaken to try to replace the surface water taken in by the trap, on its descent, with the water at depth. Then the traps, in baskets, were screwed onto the posts. For the 1982 experiments, the contents of the trap were displaced by air from a SCUBA tank just before the trap was placed on a post. At the end of the trap collecting interval, the screens on the traps and the funnels in traps OPF8.9-2.0, OPF12.2-1.7, OPF15.8-1.4, and TBF14.7-1.6 were carefully removed and the traps were capped in place and transported to the surface.

4.2.2 A priori hypotheses concerning trap collections of larvae

From two to five trap designs were simultaneously deployed in

the field. Of the seven trap collecting intervals in 1980 and the ten trap collecting intervals in 1982, results for a total of seven intervals are reported here. Information about these intervals (the duration, the trap designs tested, the transects used, and the availability of current meter data) are listed in Table 4.1. Results reported here for collections during the summer of 1980 were for three traps (OPC7.7-1.1, OPC7.7-2.1, and OPF8.9-2.0) very similar in design and dimensions to the Group C traps (compare trap diagrams in Figures 4.10 and 3.31) tested in the flume. In addition, two other funnel trap designs (OPF12.2-1.7 and OPF15.8-1.4) were deployed simultaneously with the Group C-like traps. The dimensions of all five trap designs deployed in the summer of 1980 are given in Table 4.2 and the traps are diagramed in Figure 4.10.

Specific a priori hypotheses concerning larval collections by the groups of trap designs deployed during the collecting intervals (see Table 4.1) are given below. The hypotheses were stipulated from the flume experiments (see especially Section 3.3.6).

(1) Group A traps: If larvae sink through near-bottom waters like passive particles then trap OPG8.3-3.0 should collect relatively more larvae per unit mouth area than trap OPC8.5-2.7 (see Figure 3.27).

(2) Group B traps: If larvae sink through near-bottom waters like passive particles then the rank order of larval collections by the Group B traps should be OPG8.3-3.0 > OPC8.5-2.7 > OPP8.3-2.7 (see Figure 3.30).

(3) Group C-like traps: If larvae sink through near-bottom

TABLE 4.1

Information about the Nine Separate Trap Collection Intervals for which Results are Reported

Date traps retrieved	Length of collecting interval (days)	Transects used[1]	Trap designs tested[2]	Current meter data available for interval
8/25/80	11	1980	Group C-like	no
7/27/82	4	1982A	Group A	yes
8/20/82	4	1982B	Group D	yes
9/15/82	1	1982B	Group A and TBC14.7-1.6S	yes
9/20/82	5	1982B	Group B	yes
9/21/82	1	1982B	Group A and TBC14.7-1.6S	yes
9/22/82	1	1982B	Group A[3]	yes

1. For "1980" see Figure 4.3, for "1982A" see Figure 4.4A, and for "1982B" see Figure 4.4B.
2. See Figure 3.26 for traps in Group A, Figure 3.29 for traps in Group B, Figure 4.10 for the Group C-like traps, and Figure 3.33 for traps in Group D (trap TBC14.7-1.6S is in this group).
3. Traps in Group B were deployed during this interval but replicates for trap OPP8.3-2.7S were not sorted.

TABLE 4.2

Dimensions of Traps Deployed in the Summer of 1980

Trap design	Trap code	Wall thickness (mm)	Total trap height (cm)	Inside mouth diameter (cm)	Aspect ratio[1]	Inside diameter at bottom of funnel (mm)	Funnel height	Cylinders holding the funnels[2] Inside diameter (cm)	Height (cm)
Opaque plastic cylinder	OPC7.7-1.1	0.1	8.7	7.7	1.1				
Opaque plastic cylinder	OPC7.7-2.1	0.1	16.4	7.7	2.1				
Opaque plastic cylinder with funnel in mouth	OPF8.9-2.0	0.1	18.0	8.9	2.0	13±3	71±5	8.5	16.4
Opaque plastic cylinder with funnel in mouth	OPF12.2-1.7	0.1	20.2	12.2	1.7	23±2	92±2	8.5	16.4
Opaque plastic cylinder with funnel in mouth	OPF15.8-1.4	0.1	22.7	15.8	1.4	18±1	123±1	8.5	16.4

1. Ratio of total trap height to inside mouth diameter.
2. Funnels were rested in the mouth openings of the cylinders (so the bottom of the funnels stuck into and below the cylinder mouth) and screens, covering the funnel mouth, were hose-clamped around the cylinders to hold the funnels in place.

waters like passive particles then traps OPC7.7-1.1 and OPC7.7-2.1 should collect similar numbers of larvae per unit mouth area and trap OPF8.9-2.0 should undercollect larvae compared to these two trap designs (see Figure 3.32). Traps similar in design or dimensions to traps OPF12.2-1.7 and OPF15.8-1.4 (see Tables 3.1 and 4.2) were never tested in the flume study, so a priori predictions regarding larval collections by these funnel trap designs cannot be made.

(4) Group D traps: If larvae sink through near-bottom waters like passive particles then traps OPC8.5-2.7, TBC14.7-1.6 and TBF14.7-1.6 should collect similar numbers of larvae per unit mouth area (see Figure 3.34). Note, however, that traps TBC14.7-1.6 and TBF14.7-1.6 tended to have lower particle collection efficiencies relative to trap OPC8.5-2.7, during the flume experiments. All three replicate collection efficiencies of trap TBC14.7-1.6 were less than the three collection efficiencies of trap OPC8.5-2.7 during series 8/24/82 (Figure 3.34). However, these collections were not considered different statistically because the within-trap design variability (CV ~ 1.9 percent) in collections by trap TBC14.7-1.6 was much less than the minimum measurement error (~ 5 percent) calculated for the flume experiments (see Section 3.3.6). Also, replicate collections by screened versions of traps OPC8.5-2.7 and TBF14.7-1.6 did not overlap if the funnel-washings from trap TBF14.7-1.6 were not included as part of the trap samples.

(5) Group A traps and trap TBC14.7-1.6: If larvae sink through near-bottom waters like passive particles then trap OPG8.3-3.0 should overcollect larvae when compared to traps OPC8.5-2.7 and TBC14.7-1.6

(see Figures 3.27 and 3.34); the latter two trap designs should collect similar numbers of larvae per unit mouth area or trap TBC14.7-1.6 should be an undercollector compared to trap OPC8.5-2.7 (see previous paragraph).

4.2.3 Samples taken and sampling schedule

In addition to trap samples, the sediments were sampled for organisms at the beginning and at the end of each trap collecting interval. The benthos was sampled with five butyrate corers (65-mm inside diameter) inserted into the sediment to a depth > 10 cm, when possible. The top 10 cm of the core was vertically sectioned into approximately 2-cm layers (see Section 4.2.4). The sandy and compact nature of the bottom sediments at this station made it impossible to manually push cores to > 10-cm depth in the sediment, so a weight (~ 2250 g) was used to pound the cores into the sediment. Samples were taken as quickly as possible to minimize the escape of organisms through the bottom of the core. The surface and upper subsurface components of the fauna (e.g., newly settled larvae) were of primary interest in this study, so once during each summer several cores were taken without using the weight (so only the top ~ 5 cm of sediment was sampled) to determine if organisms in the upper layers of the sediment redistributed in response to pounding by the weight. The cores were placed upright in a rack and maintained in this vertical orientation during transport to the surface.

During the summer of 1980, the cores were taken at haphazardly located positions about halfway between two of the transect lines. The five cores were placed, adjacent to each other, in a straight

line paralleling the transects (that is, running ~ 60° magnetic). During the summer of 1982, the five cores were taken at a particular post location along a transect line, as determined from a random number table. The cores were taken, as a group, within an ~ 625-cm^2 area about 2 m to the northwest (except for the 330° transect line shown in Figure 4.4A: cores were taken to the southwest of posts on this line) side of the posts.

Sediment samples were also taken periodically (usually every two weeks) during each summer. Butyrate corers used for sediment samples were 22 mm in inside diameter and were inserted about 5-cm deep into sediments (no pounding was required using these small corers). Usually only the top 2 cm of the sediment was saved for sediment analyses (see Section 4.2.4). Replicate cores were taken about a meter to the southeast of posts on the various transect lines (except for the 330° transect line shown in Figure 4.4A: cores were taken to the northeast of posts on this line). Sometimes cores were taken at every post location and sometimes cores were taken at every other post location. Cores were placed upright in racks and maintained in this vertical orientation during transport to the surface.

Even though the sediments at the study site have been characterized as primarily medium sands (see Section 4.1.2), direct observations of the sediment surface indicate that a mud veneer 1- to 2-cm thick rests on this bed of sand. This mud is easily resuspended off the bed and was virtually absent when there were strong bottom currents (personal observations). Because larvae are expected to be initially deposited in these surficial sediments,

great care was taken to insure that these sediments were quantitatively sampled. Thus, all cores for organisms and for sediments were taken on the first dive at the study site on a given day and usually were taken before the area to be cored had been visited by any divers. Cores were also slowly and carefully inserted into sediments to try to keep the surface flocculated material intact.

4.2.4 Sample processing

By the time the retrieved traps were returned to the laboratory for processing, the visible suspended sediment had fallen to the bottom of the trap. For the 1980 samples, about half of this clear seawater was discarded before each sample was processed. Because most of the larvae collected in the traps were metamorphosed and/or in tubes in the sediment (see Section 4.3.1), it is unlikely that they were swimming around in this discarded water. However, to be conservative, for the 1982 samples, the overlying water was not discarded and the entire trap sample was processed.

The 1980 trap samples were split twice, using a standard plankton splitter. Half of the total sample was then fixed in ~ 10 percent buffered formalin and the other two quarters were processed, separately, as sediment samples. The sediment sample splits were allowed to sit for ~ 24 hr in a cold room (6±1°C) and then the clear surface water was carefully pipetted off and the samples were frozen. Results from 1980 showed excellent replication in sediment characteristics between the two sediment splits taken from each trap (see Section 4.3.2). Thus, for all trap collections in 1982 that were longer than one day, the samples were also split twice but only

one quarter of each sample was frozen for sediment analyses. The entire contents of the one-day trap collections were treated and processed for larvae.

All larval samples from traps were fixed in formalin for two to seven days and then sieved through nested 500-, 300-, 100- and 63-μm screens into ~ 80 percent ethanol. All polychaete, mollusc, echinoderm, and enteropneust larvae and postlarvae were sorted from the samples, under a dissecting microscope, and all polychaetes were identified to lowest taxon.

The sediment samples from the 1980 trap samples were dried at 55 to 60°C to a constant weight (± 0.005 g) and then wet-sieved through a 63-μm screen. This sand fraction (the residue on the 63-μm screen) was dried and weighed. Thus, the total weight of sediments contained in half the trap sample, the percent sand, and the percent silt plus clay (or mud) was determined for the sediment samples. Results for the sediment samples from 1982 are not reported here.

The bottom cores taken for organisms were vertically sectioned into ~ 2-cm units, fixed in ~ 10 percent buffered formalin and later sieved through nested 500-, 300-, 100-, and 63-μm screens into ~ 80 percent ethanol. Results from these samples are not reported here.

The top 2 cm of sediment from the bottom sediment cores was frozen for later sediment analyses. Results from these samples also are not reported here.

4.2.5 Physical measurements using a bottom-moored tripod system

The bottom-moored tripod instrument system deployed by Dr.

Bradford Butman (U.S. Geological Survey, Woods Hole, MA) at the study site during 1982 is described in Butman and Folger (1979). Tripods were deployed for two contiguous intervals. The first tripod was deployed on 5 July 1982 and retrieved on 20 August 1982 because of severe fouling of the rotors on one of the current meters. The deployment site for this tripod was southeast of the trap transects (see locationof "Tripod A" on Figure 4.5). The second tripod was deployed on 20 August 1982 and retrieved on 5 January 1983, but the tape that recorded the data ran out on 31 October 1982. This tripod was located almost due south of the trap transects (see location of "Tripod B" on Figure 4.5).

The tripod has instruments for measuring currents, pressure, light transmission, and temperature and is equipped with a camera that takes bottom photographs. Savonius rotors for measuring current speed were located 0.5- and 1.0-m above the seabed. However, the top rotor fouled during the first tripod interval so only current speeds 0.5-m above the bottom were accurate from 5 July 1982 to 20 August 1982. Current speed and pressure were sampled in two ways (see Butman and Folger 1979); an average measurement was made over a 3.75-min interval and a "burst" of measurements were taken in the middle of this interval (24 burst measurements were taken at 2-sec intervals). The current speed and pressure measurements reported here are usually from the 3.75-min averages and the current directions are from the burst samples. Light transmission and temperature were sampled at only one time interval, at the midpoint of each 3.75-min interval. Bottom photographs were taken every hour.

4.3 Results

4.3.1 Trap collections of larvae

Trap collections of species from four invertebrate phyla are reported here. First, the abundant organisms collected in the traps are described. Second, the distributions and abundances of these organisms among the various trap designs are reported. Only results from the 500-, 300-, and 100-μm fractions of the samples are reported here; examination of several 63-μm samples indicated that, except possibly for some straight-hinge larval bivalves, very few individuals from the groups reported here are small enough to be retained in the 63-μm fraction. Occassionally, straight-hinge bivalve larvae were found in the 63-μm samples and the possibility that a large set of these larvae would be retained primarily on this screen size cannot be discounted. The percentages of organisms retained on the 500-, 300, and 100-μm screens for each trap-collecting interval are listed in Table 4.3. The percentages of organisms retained on the two larger screen sizes generally decreased with decreasing length of the trap-collecting interval, while the percentage of organisms retained on the 100-μm screen generally increased with decreasing length of the trap-collecting interval. This result suggests that the organisms feed and grow in the traps during the longer intervals.

Of the polychaete worms (Phylum Annelida, Class Polychaeta) collected in the traps, only two species consistently occurred in numbers large enough to permit meaningful statistical analyses of the samples. The two species are Mediomastus ambiseta (Hartman) from the

TABLE 4.3

Percentage of Individuals Retained on the 500-, 300-, and 100-μm Screens Relative to the Length of the Trap Collecting Intervals

Length of collecting interval (days)	Date traps retrieved	Percentage of individuals per screen size () = number collected 500 μm	300 μm	100 μm
Mediomastus ambiseta				
11	8/25/80	1.9 (20)	15.9 (166)	82.2 (858)
5	9/20/82	0.6 (3)	0.4 (2)	99.0 (486)
4	7/27/82	0.1 (1)	0.7 (6)	99.2 (878)
4	8/20/82	1.9 (4)	5.7 (15)	92.8 (245)
1	9/15/82	1.0 (3)	2.0 (6)	96.9 (285)
1	9/21/82	0 (0)	0.4 (2)	99.6 (462)
1	9/22/82	1.0 (2)	1.5 (3)	97.4 (191)
overall		0.9 (33)	5.5 (200)	93.6 (3405)
Pectinaria gouldii				
11	8/25/82	35.0 (21)	51.7 (31)	13.3 (8)
5	9/20/82	2.0 (2)	38.3 (38)	59.6 (59)
4	7/27/82	5.9 (1)	52.9 (9)	41.2 (7)

TABLE 4.3 (cont. - 2)

Length of collecting interval (days)	Date traps retrieved	Percentage of individuals per screen size () = number collected 500 μm	300 μm	100 μm
Pectinaria gouldii (cont.)				
4	8/20/82	31.9 (22)	39.1 (27)	27.5 (19)
1	9/15/82	0 (0)	15.8 (3)	84.2 (16)
1	9/21/82	0.1 (1)	7.8 (7)	91.2 (83)
1	9/22/82	0 (0)	22.5 (9)	77.5 (31)
overall		11.9 (47)	31.5 (124)	56.6 (223)
Sabellarids				
5	9/20/82	0 (0)	5.1 (2)	94.9 (37)
4	7/27/82	0 (0)	34.6 (9)	65.4 (17)
4	8/20/82	3.8 (1)	0 (0)	96.2 (25)
1	9/15/82	0 (0)	4.1 (8)	95.9 (187)
1	9/21/82	0 (0)	18.2 (6)	81.8 (27)
1	9/22/82	0 (0)	21.7 (10)	78.3 (36)
overall		0.3 (1)	9.6 (35)	90.1 (329)

TABLE 4.3 (cont. - 3)

Length of collecting interval (days)	Date traps retrieved	Percentage of individuals per screen size () = number collected 500 µm	300 µm	100 µm
Bivalves				
5	9/20/82	7.7 (23)	7.4 (22)	84.8 (252)
4	7/27/82	1.4 (10)	7.4 (52)	91.2 (640)
4	8/20/82	5.9 (41)	12.0 (83)	82.1 (568)
1	9/15/82	11.4 (14)	4.1 (5)	84.6 (104)
1	9/21/82	3.2 (3)	6.4 (6)	90.4 (85)
1	9/22/82	0 (0)	1.6 (2)	98.4 (123)
overall		4.5 (91)	8.4 (170)	87.2 (1772)
Enteropneusts				
4	7/27/82	0 (0)	5.1 (4)	94.9 (75)
4	8/20/82	6.1 (2)	3.0 (1)	90.9 (30)
overall		1.8 (2)	4.5 (5)	93.8 (105)
Seastars				
4	8/20/82	0 (0)	2.4 (14)	97.6 (561)

Family Capitellidae and Pectinaria gouldii (Verrill)[1] from the Family Pectinariidae, hereafter refered to as "Mediomastus" and "Pectinaria", respectively. All Mediomastus were metamorphosed postlarvae and many were found inside mucus sheaths (the tube structure that they drag along with them when burrowing through sediments) with sand grains attached. About 94 percent of the individuals were retained in the 100-μm fraction of the samples (Table 4.3). Pectinaria collected by traps were also metamorphosed post-larvae. Most individuals were found inside their characteristic ice-cream-cone-shaped tubes. In the one-day collection (see Table 4.1) the tubes consisted only of the opaque parchment-like material that the worms evidently secrete while still in the plankton (Lacalli [1980] reported that metamorphosed Pectinaria granulata [Linne][2] in tubes were collected from the plankton). However, sand grains were attached to the anterior ends of the tubes collected in traps left in the field for longer periods of time (see Table 4.1). About half of the Pectinaria individuals were collected in the combined 500- and 300-μm fractions and about half were collected in the 100-μm fractions (Table 4.3).

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1. According to Hartman (1941), the genus Pectinaria Lamarck can be divided into the two subgenera, Pectinaria Malmgren and Cistenides Malmgren. The species referred to in the present study as Pectinaria gouldii (Verrill) belongs to the subgenus Cistenides and, thus, is called Cistenides gouldii by some authors (e.g., Whitlatch and Weinberg 1982).
2. Pectinaria granulata (Linne) is also in the subgenus Cistenides according to Hartman (1941).

Polychaetes from the Family Sabellariidae also were relatively abundant in the trap samples. About 90 percent of the individuals were collected in the 100-μm fraction of the samples (Table 4.3). The organisms collected were still in the unmetamorphosed pelagic larval stage. Larvae of Sabellaria vulgaris Verrill, the only sabellarid previously collected in bottom samples at Station 35 (Sanders et al., 1980), do not metamorphose until they are about 550-μm and ~ 6-setigers long (Eckelbarger 1975). Most of the sabellariid larvae collected in traps were identifiable only to family by their provisional bundles of barbed setae protruding from the head region (or "episphere," see Eckelbarger 1975); the individuals were usually only one or two segments long. Segments with setae were rarely present. In Eckelbarger's (1975) description of the late pelagic larva of Sabellaria vulgaris, he notes that two achetigerous thoracic segments follow the episphere and then the setigers begin. The sabellariids collected in this study are probably Sabellaria vulgaris, but they are referred to as "sabellariids" because confirmed identifications are presently impossible for these early larval stages.

Bivalves (Phylum Mollusca, Class Lamellibranchia, Pelecypoda, or Bivalvia) were always abundant in trap samples. Most individuals were very small (~ 87 percent were collected in the 100-μm fraction of the samples, Table 4.3) and some were collected as veligers, in the relatively undifferentiated "straight-hinge" larval stage. Larval bivalves are notoriously difficult to identify, even to family, in some cases (but see Rees 1950; Chanley and Andrews 1971), and no

attempt was made here to separate bivalves into lower taxonomic units.

Two other taxa were abundantly collected in traps during one or more trap-collecting intervals: enteropneusts or acorn worms (Phylum Hemichordata, Class Enteropneusta) and seastars (Phylum Echinodermata, Class Asteroidea). About 94 percent of the acorn worms were collected in the 100-μm fraction of the samples. The individuals possess the characteristic constrictions dividing the probosis from the collar region and the collar from the remainder of the trunk; thus, they are no longer in the tornaria larval stage and are considered metamorphosed postlarvae. Enteropneusts were occassionally collected by Sanders et al. (1980) in bottom samples at Station 35 (J.F. Grassle, personal communication); although they are probably Saccoglossus, these were not definitively identified to genus. The acorn worms collected here are referred to as "enteropneusts".

The seastars collected in the traps were almost exclusively (about 98 percent, Table 4.3) found in the 100-μm fractions of the samples. All organisms were undergoing metamorphosis from the brachiolaria larval stage. In most of the specimens the stalk (three brachiolar arms and the sucker for attachment) and the primordium of the definitive star can be seen. Both structures are in various stages of development among the specimens. However, none of the individuals were completely metamorphosed (i.e., the stalk was always present, in some form). These metamorphosing larvae are probably from the genus Asterias because postlarval and adult Asterias were occassionally collected in Sander's et al.'s (1980) study (J.F. Grassle, personal communication). However, to be conservative, they

are referred to here as simply "seastars."

In the following description of larval collections in the trap samples, the various trap-collecting intervals are referred to by the dates that the traps were retrieved from the field (see Table 4.1). Whether or not trap designs deployed simultaneously collected significantly different numbers of individuals is usually obvious from graphs of the data; statistical tests of differences in collections between or among trap designs are trivial, in most cases, because either the replicate abundances do not overlap or they overlap completely. Nonetheless, probabilities associated with rejecting the null hypothesis of no difference in collections between or among the trap designs are given below the graphs (Figures 4.6, 4.8, 4.9, 4.12, 4.13, and 4.14). Nonparametric statistics were used to analyze the data (see Section 3.2.8). When results for two trap designs are reported, the Mann-Whitney U test was used. For tests among three trap designs, the Kruskal-Wallis one-way analysis of variance was used. Note that when tied values occur for small sample sizes (e.g., N = 3 or 4) using the Mann-Whitney U test, two values of the U statistic were calculated here and, thus, two probabilities are given below the graphs (e.g., see the graph for Pectinaria in Figure 4.6). The two U statistics are calculated by assuming that the tied values are actually different from each other, in one direction or in the other, a procedure suggested by Siegel (1956) for treating tied values at small sample sizes.

During interval 7/27/82 (a four-day collection), collections of Mediomastus, sabellariids, bivalves and enteropneusts were

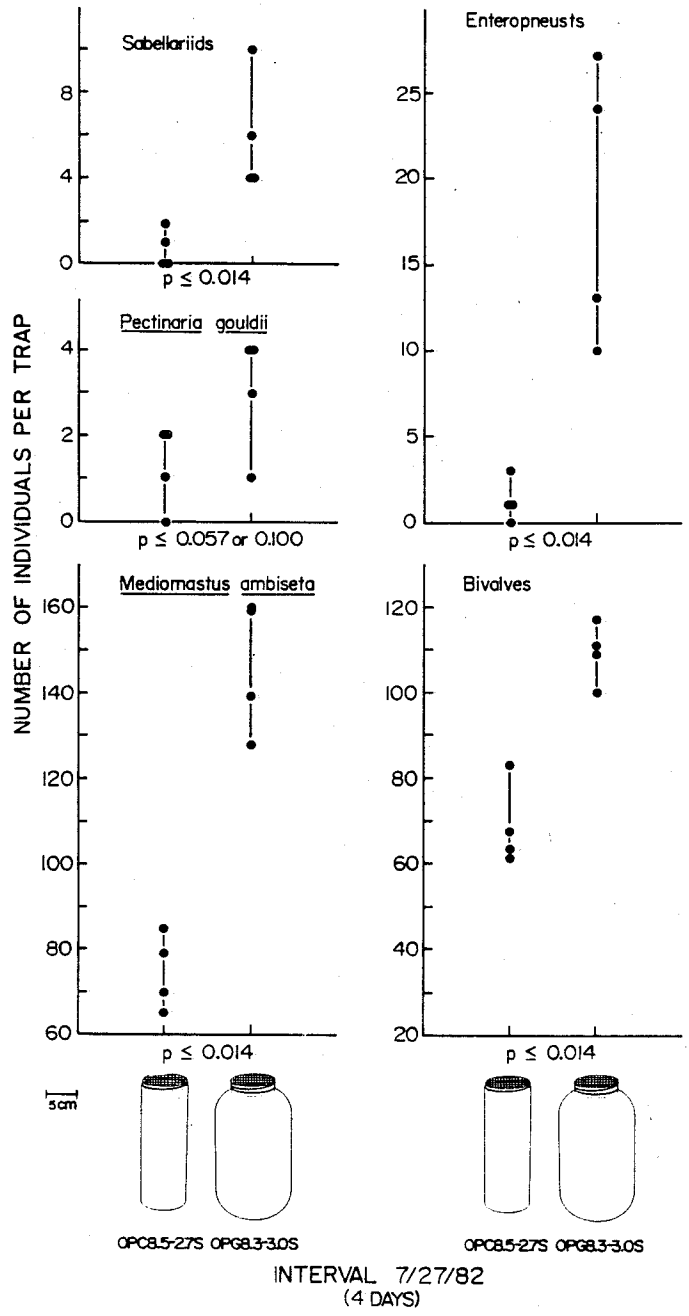

Figure 4.6: Collections of Mediomastus, Pectinaria, sabellariids, bivalves (not including straight-hinge larvae), and enteropneusts in the Group A traps deployed from 7/23/82 to 7/27/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Mann-Whitney U tests of the results.

significantly less (the H_0 could be rejected at $p \leq 0.014$) in trap OPC8.5-2.7S than in trap OPG8.3-3.0S; collections of the four groups did not overlap between these trap designs (Figure 4.6). Fewer Pectinaria also were collected in trap OPC8.5-2.7S than in trap OPG8.3-3.0S, but the H_0 could be rejected only at $p \leq 0.057$ or 0.100. These results support the a priori hypothesis stipulated from the flume experimentss for the Group A traps, that the trap OPG8.3-3.0 is an overcollector of passive particles relative to trap OPC8.5-2.7 (see [1] in Section 4.2.2).

A potential fish predator on larvae in traps was also collected during the 7/27/82 interval, juvenile cunners in the Family Labridae (probably Tautogolabrus adspersus [Walbaum]). More fish were collected in replicates of trap OPC8.5-2.7S than in replicates of trap OPG8.3-3.0S. A significant negative correlation (the H_0 of no correlation between the data was rejected a $p \leq 0.01$ using the nonparametric Spearman rank correlation) between the abundances of Mediomastus ($r_s = -0.91$) and bivalves ($r_s = -0.90$) and the abundances of fish is evident in the data (Figure 4.7). However, this predation effect alone cannot account for the approximately two-fold differences in mean collections of Mediomastus and bivalves between traps OPC8.5-2.7S and OPG8.3-3.0S. For example, a replicate of trap OPC8.5-2.7S containing only one fish collected 85 Mediomastus, but replicates of trap OPG8.3-3.0S containing only one fish each collected 128 and 139 Mediomastus (Figure 4.7).

For the Group A traps deployed for only one day (interval 9/22/82), significantly fewer sabellariids ($p \leq 0.050$) and bivalves

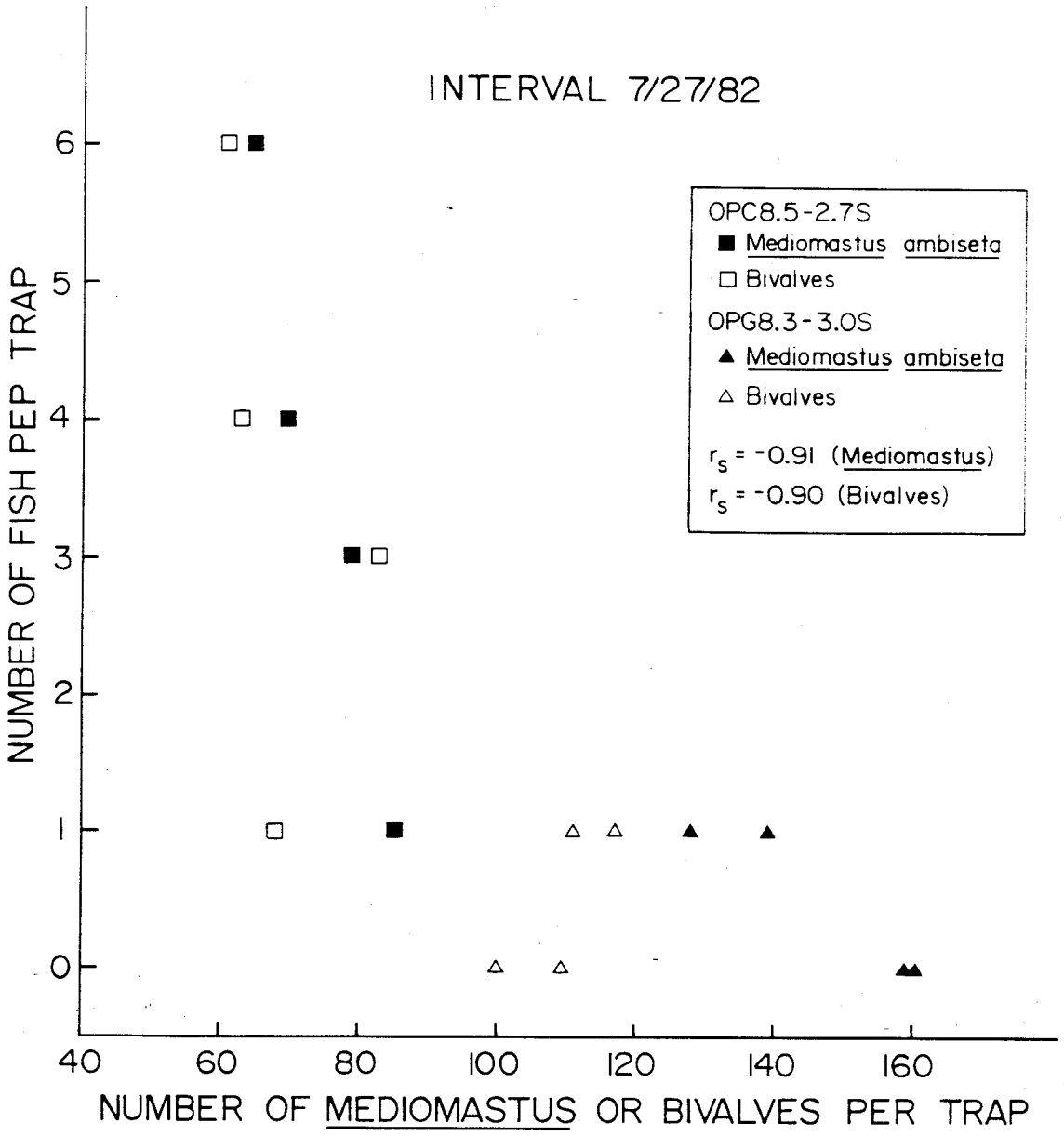

Figure 4.7: Relationship between the number of juvenile cunners and the number of Mediomastus and bivalves collected in traps OPC8.5-2.7S and OPG8.3-3.0S during the 7/27/82 interval. The Spearman rank correlation coefficients (r_s) for the data are listed on the graph. The H_0 of no correlation between the data could be rejected, in both cases, at $p \leq 0.01$.

($p \leq 0.050$ or 0.100) were collected in replicates of trap OPC8.5-2.7S than in replicates of trap OPG8.3-3.0S (Figure 4.8). This relative overcollection of organisms by trap OPG8.3-3.0S is also suggested in the data for Mediomastus and Pectinaria, but there is more overlap in the data (e.g., the H_0 could be rejected only at $p \leq 0.100$ for Mediomastus collections and at $p \leq 0.100$ or 0.250 for Pectinaria collections, see Figure 4.8). Results for this collecting interval also support the a priori hypothesis of passive particle collections by the Group A traps (see [1] in Section 4.2.2).

Results of collections by the Group B traps during interval 9/20/82 are varied, depending on the organism(s) collected. The H_0 could be rejected ($p < 0.025$) only for collections of sabellariids by the three trap designs (Figure 4.9). All four groups of organisms (Mediomastus, Pectinaria, sabellariids and bivalves) collected in these trap designs were less abundant in replicates of trap OPC8.5-2.7S than in replicates of trap OPG8.3-3.0S; in fact, collections by these two trap designs did not overlap (Figure 4.9). These results were predicted by the a priori hypothesis for collections of passive particles by Group A traps (see Figure 3.27). However, the a priori hypothesis for collections of passive particles by the Group B traps stipulated that trap OPP8.3-2.7 would collect significantly fewer organisms than trap OPC8.5-2.7 (see [2] in Section 4.2.2). This hypothesis is not supported by most of the data; collections of Mediomastus, Pectinaria and bivalves in trap OPP8.3-2.7S overlapped with collections in trap OPC8.5-2.7S and the H_0 could be rejected only at $p < 0.121$, $p < 0.286$ and $p < 0.129$ for

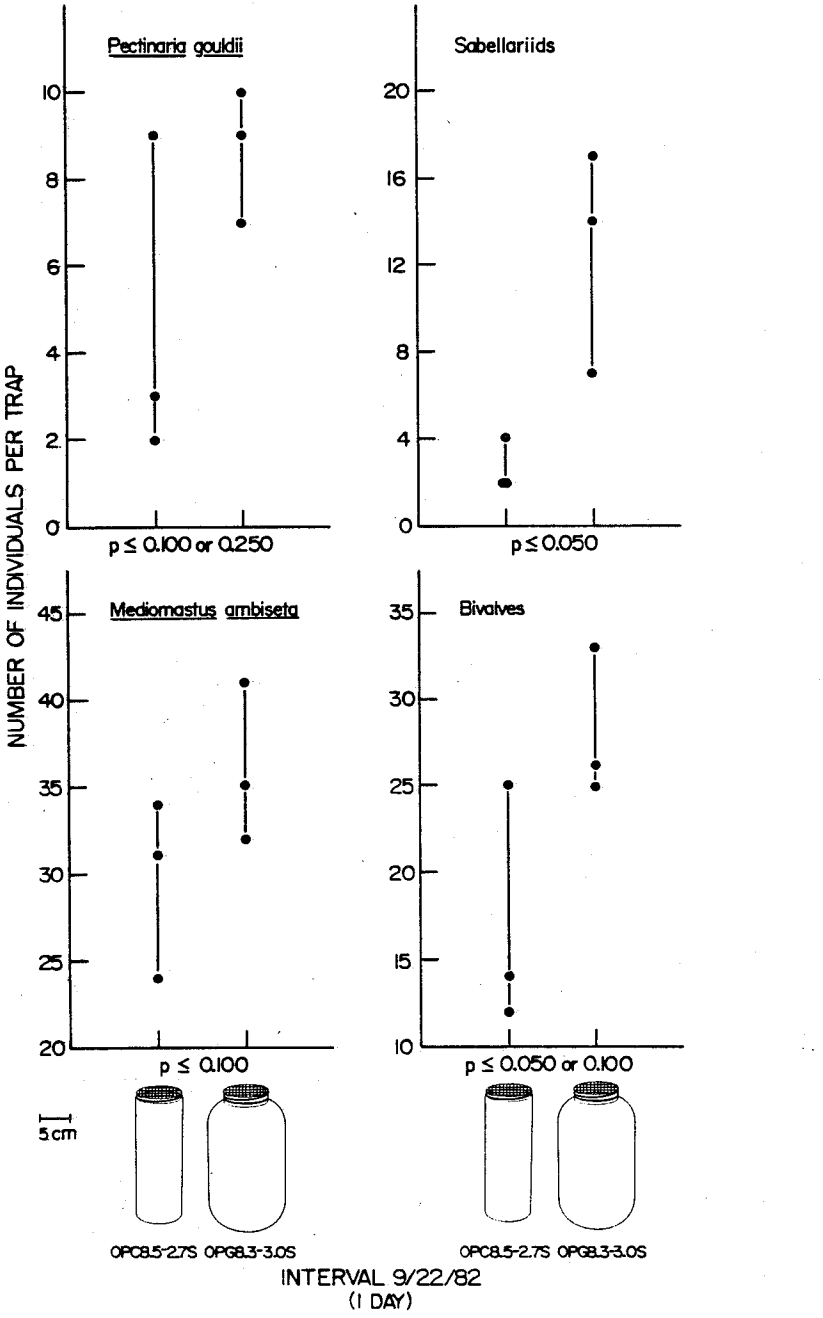

Figure 4.8: Collections of Mediomastus, Pectinaria, sabellariids and bivalves (including straight-hinge larvae) in the Group A traps deployed from 9/21/82 to 9/22/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Mann-Whitney U tests of the results.

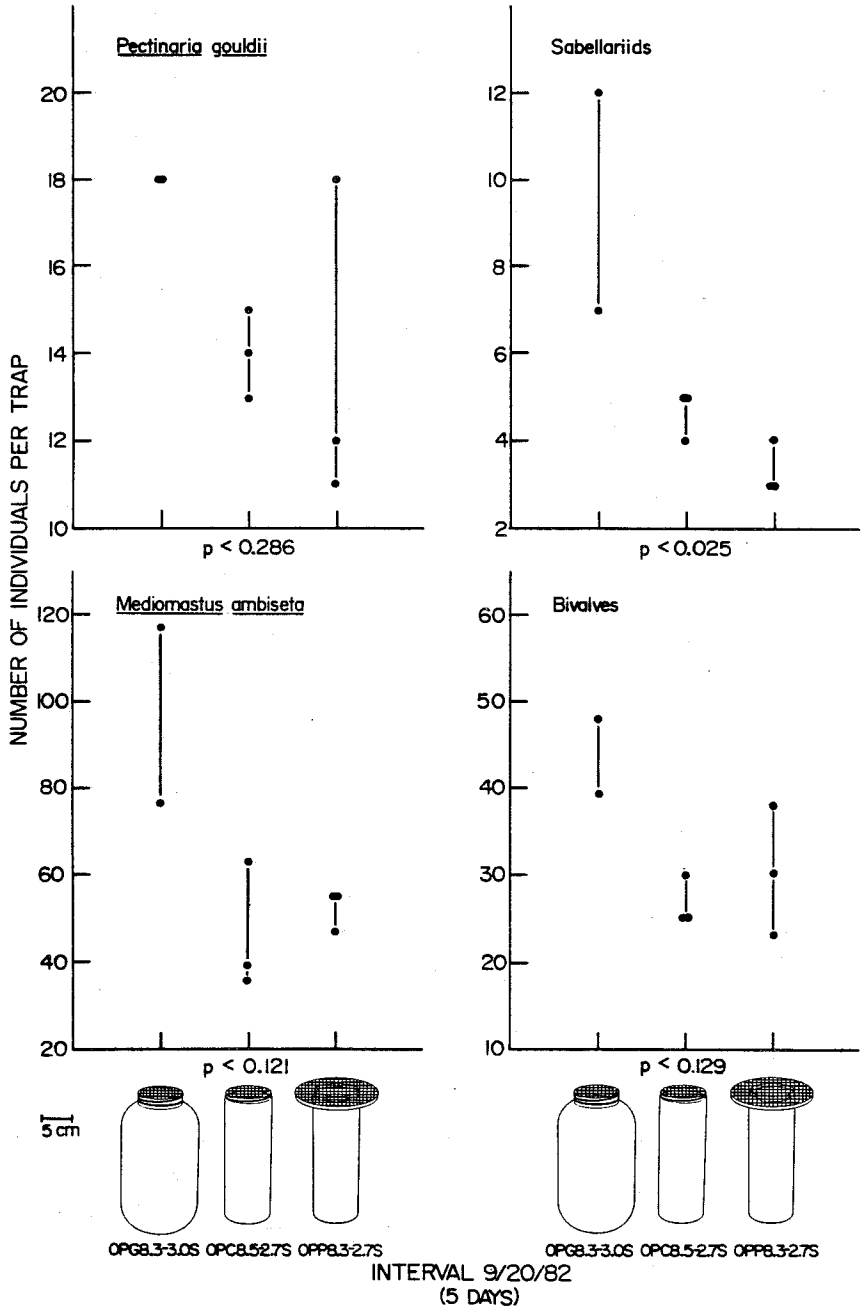

Figure 4.9: Collections of Mediomastus, Pectinaria, sabellariids and bivalves (not including straight-hinge larvae) in the Group B traps deployed from 9/15/82 to 9/20/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Kruskal Wallis tests of the results.

the organisms, respectively (Figure 4.9).

Collections of Mediomastus in all three Group C-like trap designs were significantly higher (i.e., the collections did not overlap) in traps raised 47- to 61-cm above the seabed than in traps raised $\geq$ 104-cm above the bed (Figure 4.10) during the 8/25/80 collecting interval. However, this trend was not apparent for collections of Pectinaria (Figure 4.11). At each of the three trap heights, collections of Mediomastus in traps OPC7.7-1.1S and OPC7.7-2.1S completely overlapped while collections of Mediomastus in trap OPF8.9-2.0S were always significantly lower (Figure 4.10). These results support the a priori prediction for collections of larvae by the Group C-like traps (see [3] in Section 4.2.2). Collections of Pectinaria support the a priori hypothesis only for traps raised $\geq$ 104-cm above the seabed; for the shortest trap heights, collections of Pectinaria overlapped among the three Group C-like trap designs (Figure 4.11). Collections of Mediomastus and Pectinaria in traps OPF12.2-1.7S and OPF15.8-1.4S (tested only at the shortest rack height) overlapped with collections by the Group C-like funnel trap, OPF8.9-2.0S (Figures 4.10 and 4.11).

Collections of Mediomastus, Pectinaria, sabellariids, bivalves and enteropneusts by the Group D traps deployed during 8/20/82 (Figure 4.12) support the a priori predictions for collections by these trap designs (see [4] in Section 4.2.2); the three trap designs did not collect significantly different numbers of individuals (the H_0 could be rejected at $p < 0.086$ for Mediomastus, and only at $p < 0.511$ for Pectinaria, $p < 0.629$ for sabellariids, $p < 0.100$ for

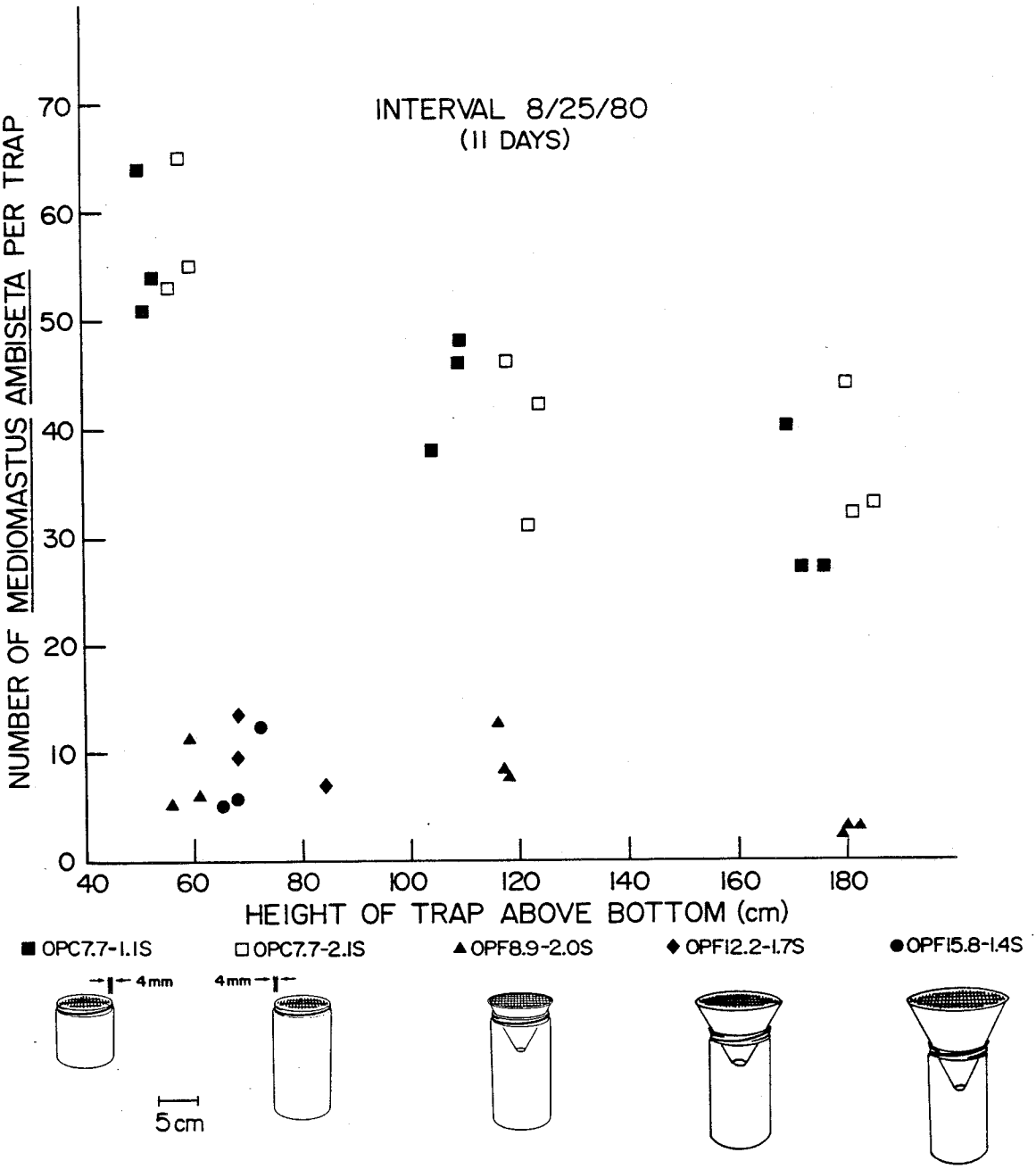

Figure 4.10: Collections of Mediomastus in the Group C-like traps and in traps OPF12.2-1.7S and OPF15.8-1.4S raised three heights above the seabed and deployed from 8/11/80 to 8/25/80. The number of organisms per 46.57 cm^2 mouth area in half of the contents of each replicate (see Section 4.2.4) are reported here. The five trap designs are drawn, to scale, below the abscissa (see also Table 2.2).

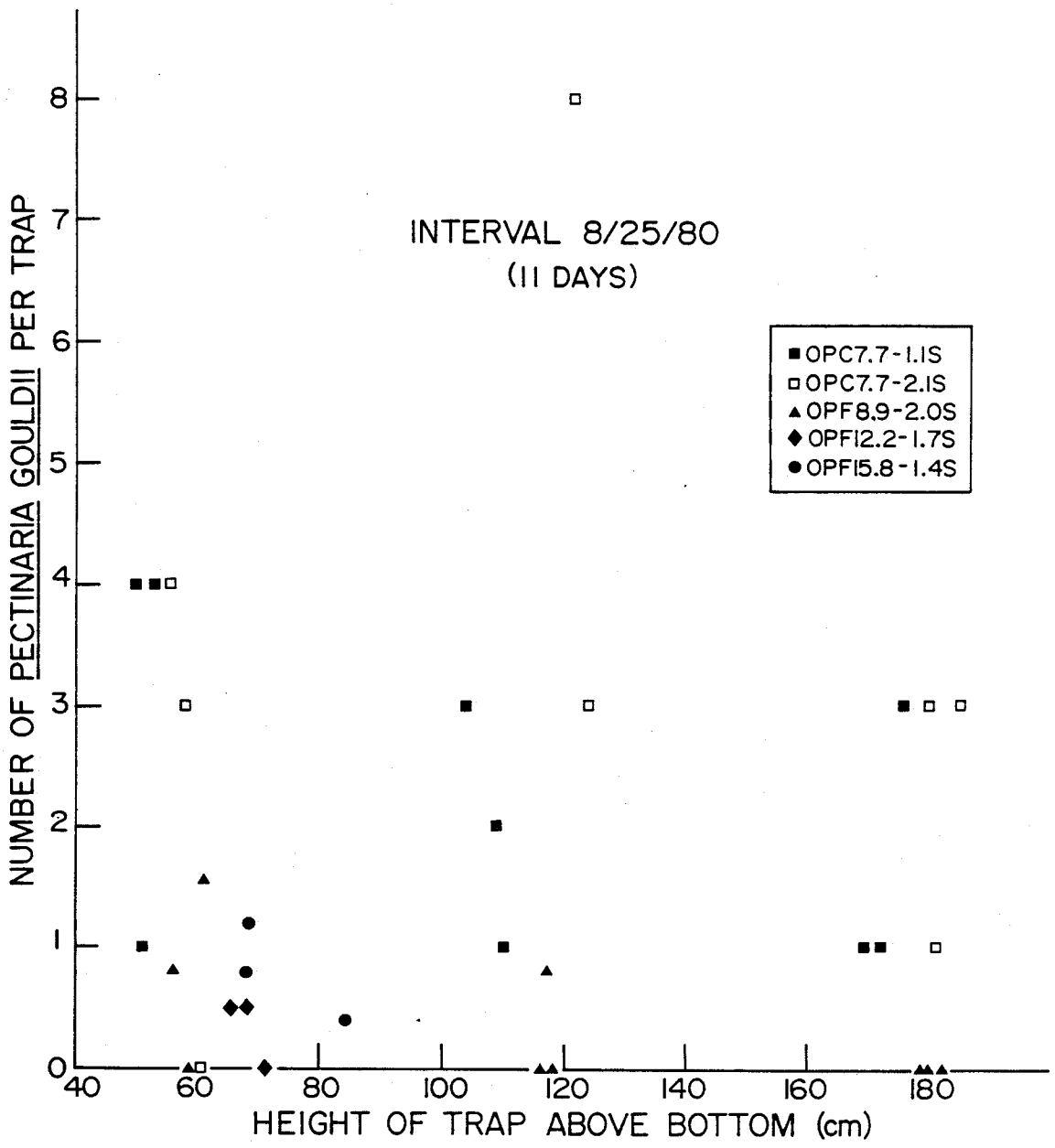

Figure 4.11: Collections of Pectinaria in the Group C-like traps and in traps OPF12.2-1.7S and OPF15.8-1.4S raised three heights above the seabed and deployed from 8/11/80 to 8/25/80. The number of organisms per 46.57 cm^2 mouth area in half of the contents of each replicate (see Section 4.2.4) are reported here. The five trap designs are diagramed in Figure 4.10.

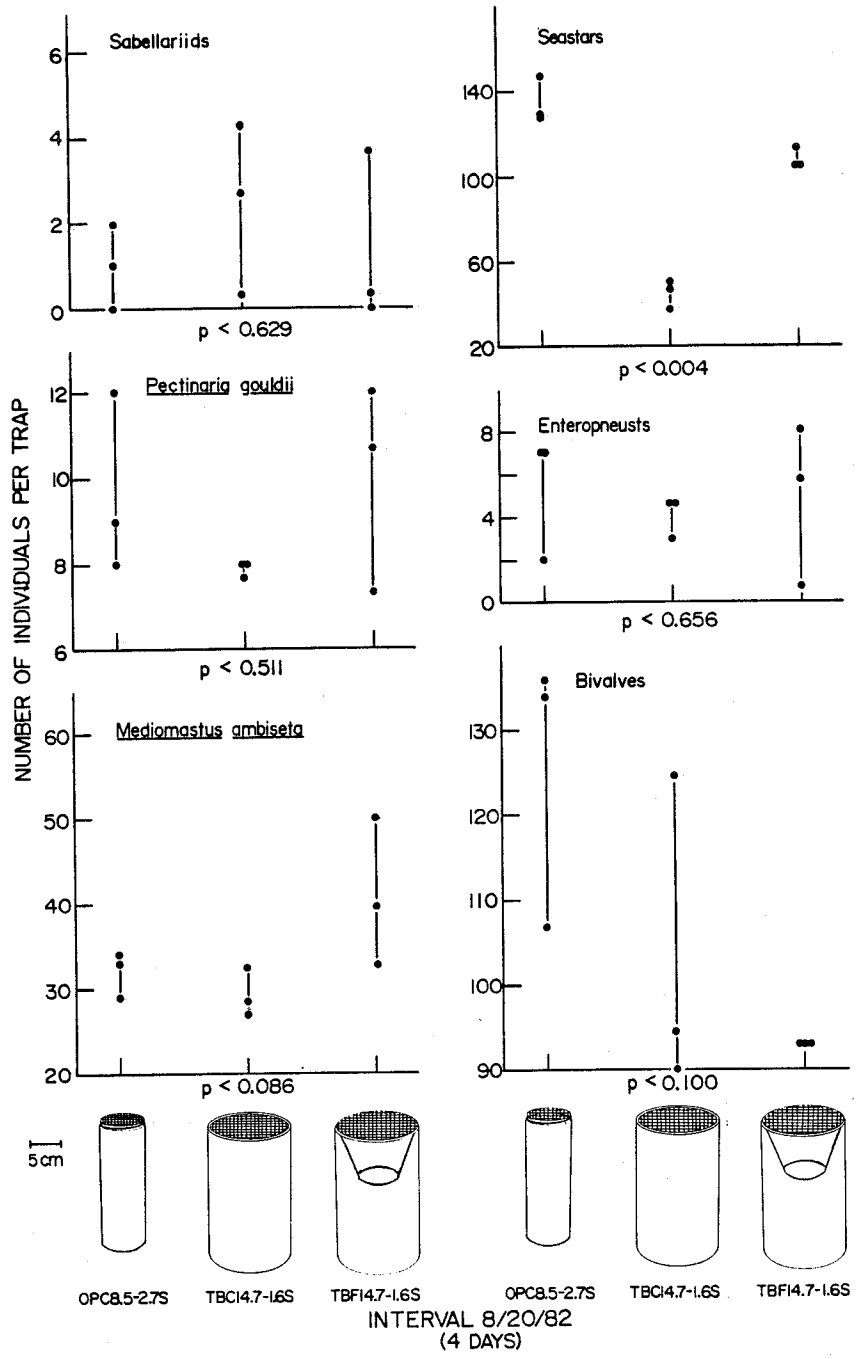

Figure 4.12: Collections of Mediomastus, Pectinaria, sabellariids, bivalves (including straight-hinge larvae), enteropneusts and seastars in the Group D traps deployed from 8/16/82 to 8/20/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Kruskal Wallis tests of the results.

bivalves and $p < 0.656$ for enteropheusts, see Figure 4.12). However, the three trap designs did collect significantly different numbers of metamorphosing seastar larvae (the H_0 could be rejected at $p < 0.004$, see Figure 4.12). Traps TBC14.7-1.6S and TBF14.7-1.6S collected significantly fewer seastars than trap OPC8.5-2.7S, a result that is consistent with the a priori predictions (see [4] in Section 4.2.2). However, overcollection of seastars by the funnel trap, TBF14.7-1.6S, compared to a cylinder with the same mouth diameter, trap TBC14.7-1.6S, violates the a priori predictions. The funnel trap also tended to collect more Mediomastus larvae than trap TBC14.7-1.6S (see Figure 4.12).

Results of collections by the Group A traps and trap TBC14.7-1.6S vary, depending on both the deployment interval and on the organisms collected. The three trap designs collected significantly different numbers of Mediomastus, sabellariids and bivalves during the one-day interval, 9/15/82 (Figure 4.13); the H_0 was rejected at $p < 0.011$, $p < 0.032$ and $p < 0.025$ for the organisms, respectively. However, for Mediomastus and bivalves, the rank order of collections by the three trap designs was OPG8.3-3.0S > OPC8.5-2.7S > TBC14.7-1.6S, but for sabellariids the rank order was OPG8.3-3.0S > TBC14.7-1.6S > OPC8.5-2.7S. Collections of Pectinaria were not significantly different ($p < 0.200$) among the three trap designs during interval 9/15/82 (Figure 4.13). The rank order for Group A traps and trap TBC14.7-1.6S collections of Mediomastus during the one-day interval, 9/21/82 (Figure 4.14), was identical to the rank order of collections during interval 9/15/82, but the H_0 could

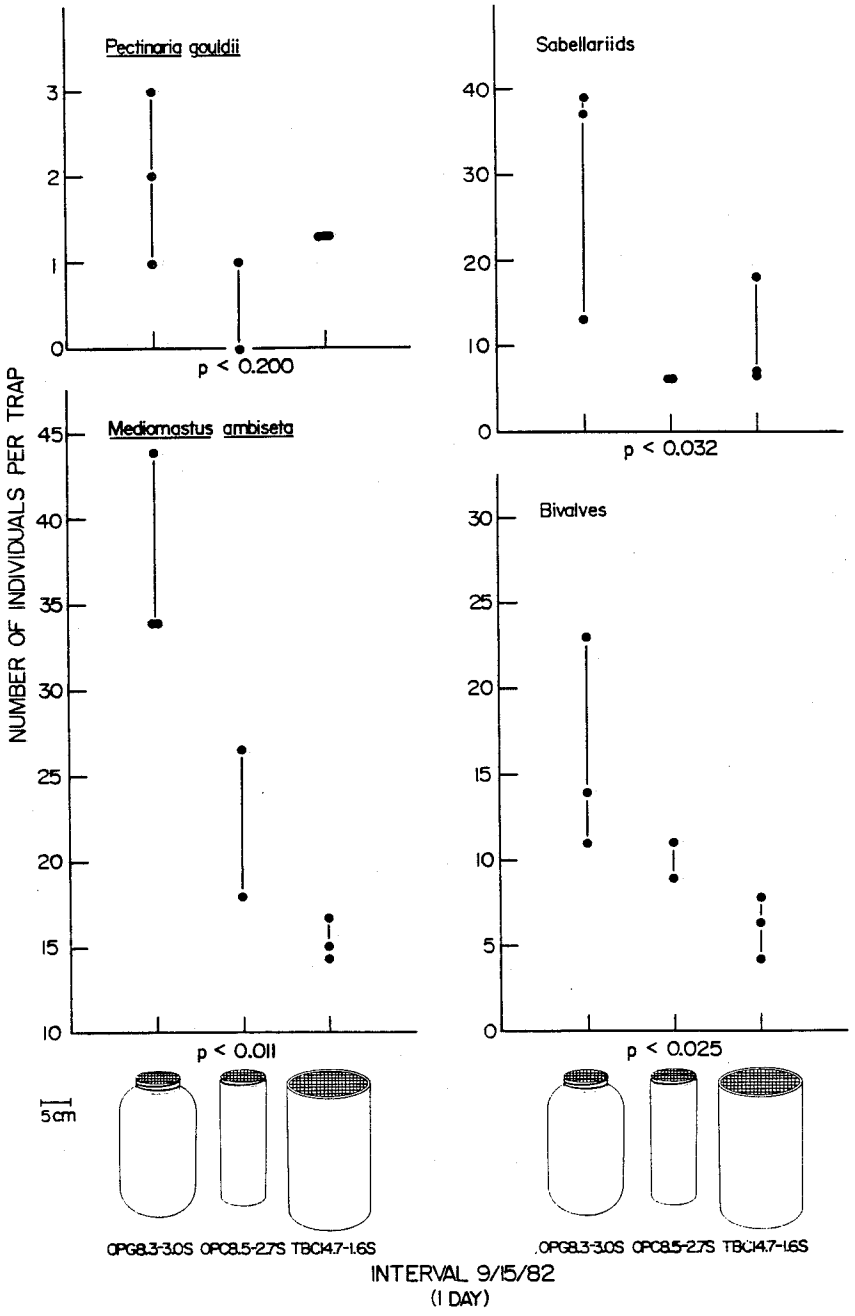

Figure 4.13: Collections of Mediomastus, Pectinaria, sabellariids and bivalves (including straight-hinge larvae) in Group A traps and trap TBC14.7-1.6S deployed from 9/14/82 to 9/15/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Kruskal Wallis tests of the results.

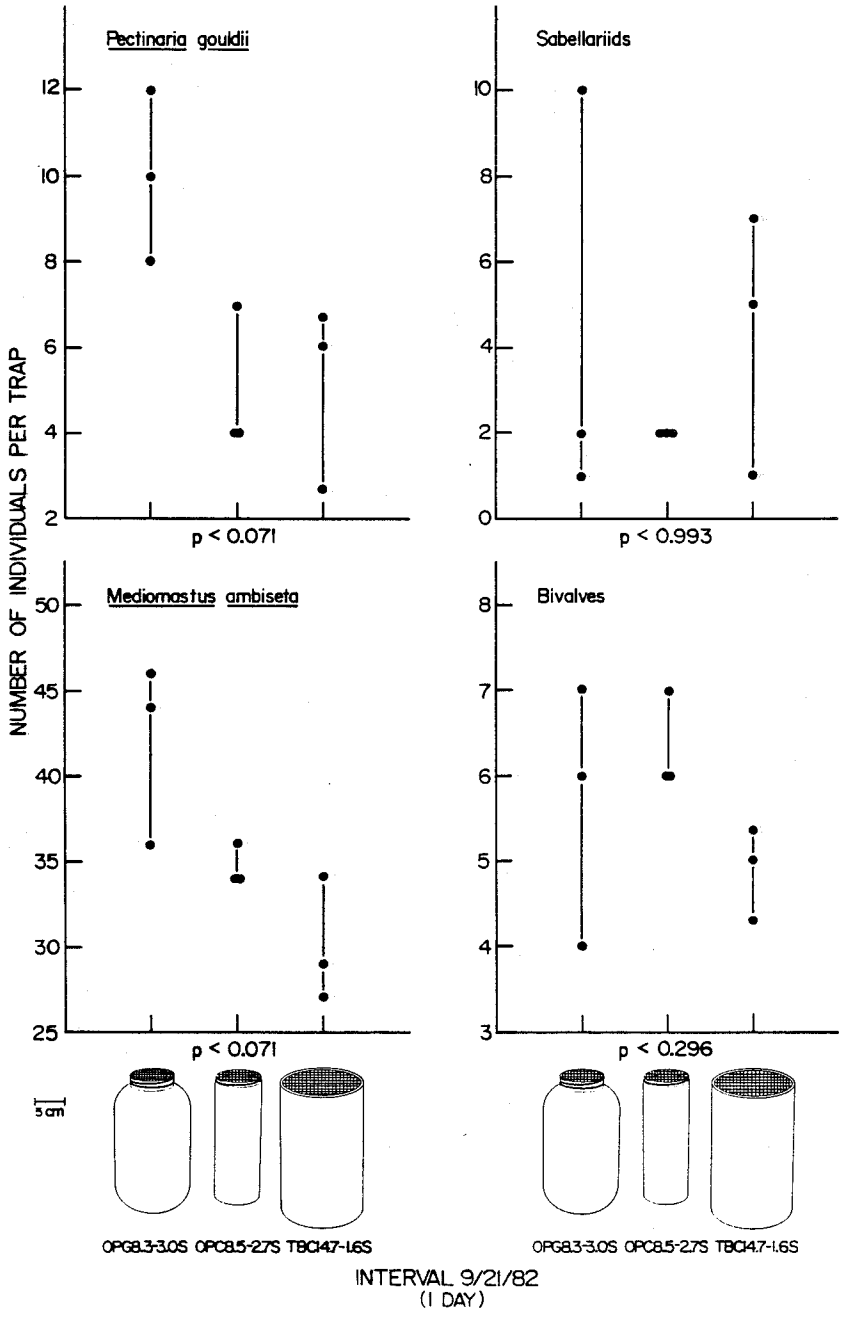

Figure 4.14: Collections of Mediomastus, Pectinaria, sabellariids and bivalves (not including straight-hinge larvae) in Group A traps and trap TBC14.7-1.6S deployed from 9/20/82 to 9/21/82. The number of organisms per 55.42 ± 2.67 cm^2 mouth area in three-quarters of the trap contents of each replicate (see Section 4.2.4) are reported here. Probabilities for rejecting the H_0 appear below each graph and are for Kruskal Wallis tests of the results.

be rejected only at $p < 0.071$ during interval 9/21/82. Collections of sabellariids and bivalves during interval 9/21/82 completely overlapped among the three trap designs (the H_0 could be rejected only at $p < 0.993$ for sabellariids and at $p < 0.296$ for bivalves) (Figure 4.14). Collections of Pectinaria were similar in traps OPC8.5-2.7S and TBC14.7-1.6S, but did not overlap and were less than collections in trap OPG8.3-3.0S during interval 9/21/82 (Figure 4.14); however, the H_0 could be rejected only at $p < 0.071$. Except for collections of sabellariids and bivalves during interval 9/21/82, the results for collections by the Group A traps and trap TBC14.7-1.6S, at least qualitatively support the a priori hypothesis for collections by these trap designs (see [5] in Section 4.2.2); traps OPC8.5-2.7S and TBC14.7-1.6S usually collected fewer larvae per unit mouth area than trap OPG8.3-3.0S, even though the trends are not statistically significant in all cases.

4.3.2 Trap collections of sediments

Results for trap collections of sediments are reported here only for the Group C-like traps and traps OPF12.2-1.7 and OPF15.8-1.4 deployed during the summer of 1980. The total weight of sediments collected in the three Group C-like trap designs decreased with increasing height above the seabed (Figure 4.15) as did collections of Mediomastus postlarvae (see Figure 4.10). Replicate collections of total sediment by traps OPC7.7-1.1S and OPF8.9-2.0S did not overlap among the three trap heights. However, for trap OPC7.7-2.1S, the total weight of sediment in traps raised 56- to 60-cm above the botom was significantly less than in all traps raised > 118-cm above

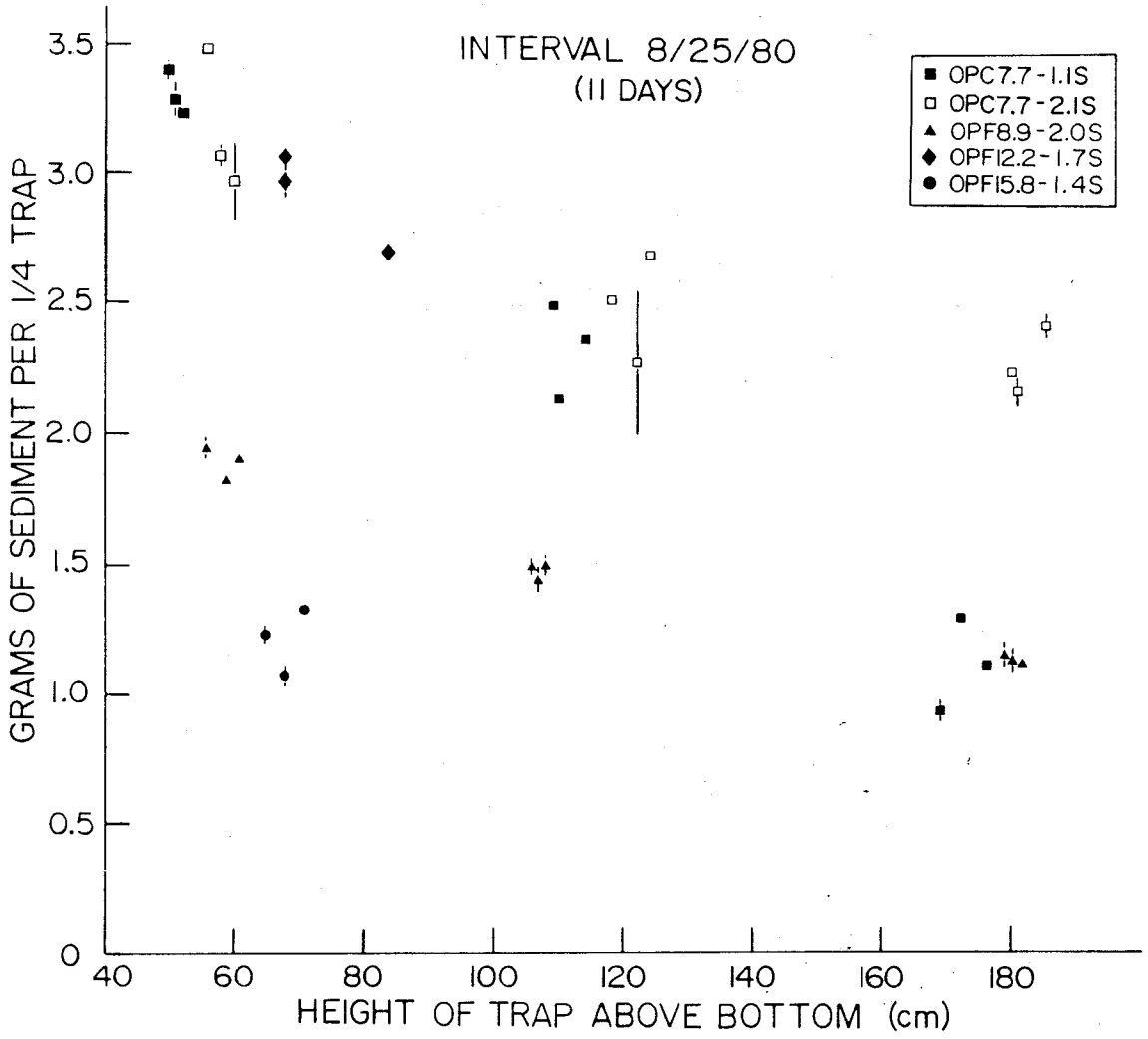

Figure 4.15: Total weight of sediment collected in the Group C-like traps and traps OPF12.2-1.7S and OPF15.8-1.4S raised three heights above the seabed and deployed from 8/11/80 to 8/25/80. The total grams of sediment per 46.57 cm^2 mouth area in two quarters, processed separately, of the contents of each replicate (see Section 4.2.4) are reported here. Vertical bars connect values for the two quarters of each replicate and mean values for these quarters are indicated by the symbols. The five trap designs are diagramed in Figure 4.10.

the bottom, but sediment collections at the two taller trap heights overlapped (Figure 4.15). The rank order of sediment collections among the Group C-like traps at the two shorter trap heights was as predicted from the flume experiments (see Figure 3.32): replicate collections by traps OPC7.7-1.1S and OPC7.7-2.1S overlapped, while replicate collections by trap OPF8.9-2.0S were always significantly lower. However, at the tallest rack height, replicate sediment collections by traps OPC7.7-1.1S and OPF8.9-2.0S overlapped while collections by trap OPC7.7-2.1S were significantly higher. Sediment collections by the other two funnel traps (OPF12.2-2.1S and OPF15.8-1.4S) tested at only the shortest rack height were significantly different from each other and from the funnel trap, OPF8.9-2.0S. Trap OPF12.2-1.7S collected more sediment per unit mouth area than trap OPF8.9-2.0S and trap OPF8.9-2.0S collected more sediment per unit mouth area than trap OPF15.8-1.4S. Collections by trap OPF12.2-1.7S overlapped with collections by trap OPC7.7-2.1S.

The percentage of mud (silt plus clay) in the sediments collected by the traps cannot be considered significantly different among any of the trap designs at the two shortest trap heights (Figure 4.16). At the tallest rack height, trap OPC7.7-2.1S contained significantly more mud than trap OPF8.9-2.0S and also tended to contain more mud than trap OPC7.7-1.1S. Variability in the percentage of mud in replicate collections by all trap designs was low (CV < 6 percent). However, replicate collections by traps OPC7.7-1.1S and OPF8.9-2.0S were generally more variable (the range in CV was 2.2 to 5.1 percent for trap OPC7.7-1.1S and 0.8 to 5.8

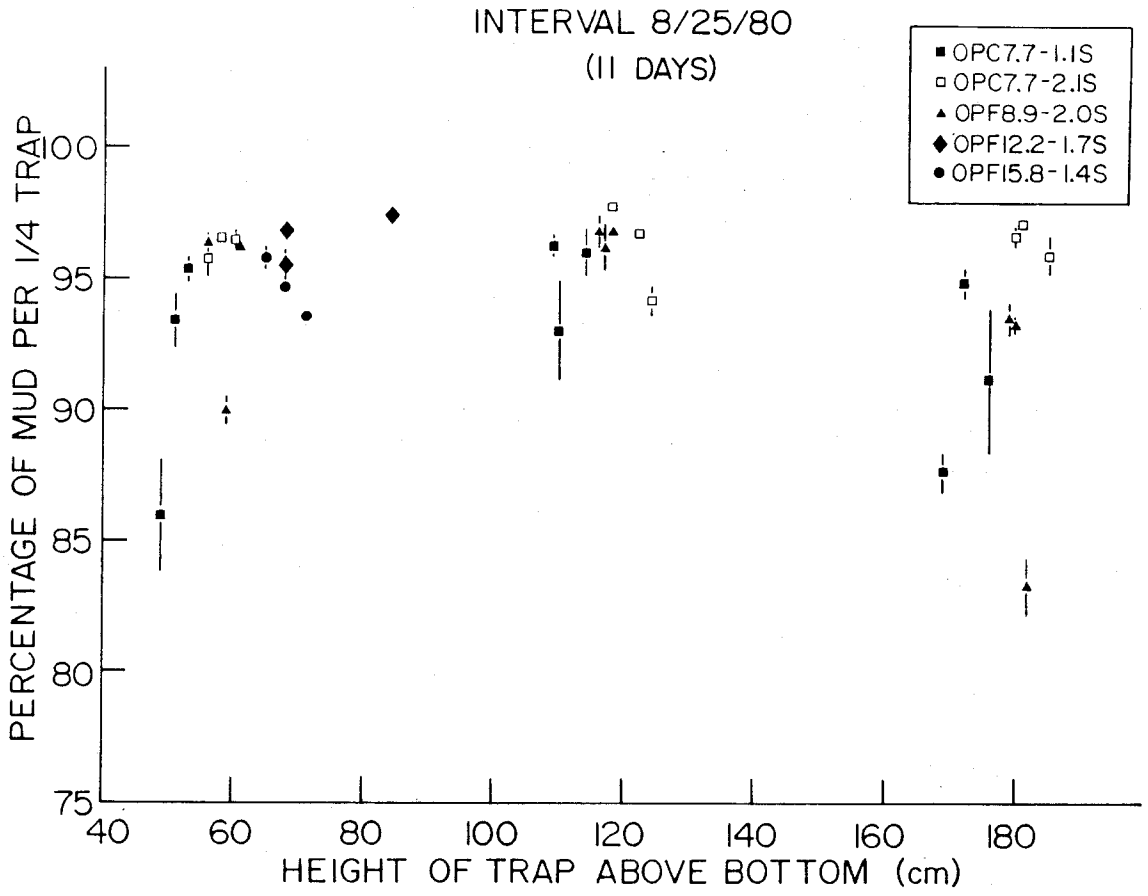

Figure 4.16: Percentage of mud (silt plus clay) in sediments collected in the Group C-like traps and traps OPF12.2-1.7 and OPF15.8-1.4 raised three heights above the seabed and deployed from 8/11/80 to 8/25/80. Two quarters of the contents of each replicate were processed separately (see Section 4.2.4); vertical bars connect values for these two quarters and the mean values are indicated by the symbols. The five trap designs are diagramed in Figure 4.10.

percent for trap OPF8.9-2.0S) than replicate collected by trap OPC7.7-2.1S at all three rack heights (range in CV was 0.7 to 1.7 percent) and for traps OPF12.2-1.7S (CV = 1.9 percent) and OPF15.8-1.4S (CV = 1.1 percent) at the shortest rack height.

4.3.3 Near-bottom current regime and other physical measurements

During the study period flows at Station 35 were primarily tidally driven at the semidurnal periodicity typical of this latitude (e.g., see "Pressure" plot in Figure 4.17). The north-south component to the near-bottom flow is much stronger than the east-west component (e.g., see top two plots in Figure 4.17), indicating that tidal flows traverse the long axis of Buzzards Bay (see Figure 4.1 and Section 4.1.2). Near-bottom currents oscillate between roughly a minimum and a maximum value twice daily (e.g., see "Speed" plot in Figure 4.18), as expected for these tidally driven flows. However, because the winds and other physical phenomena (e.g., density driven circulation or internal waves) also contribute to the flows, smooth curves oscillating between semidiurnal flow minima and maxima do not occur. Periodically, surface storm activity was detected in the near-bottom flows at the study site (e.g., see the peak in the pressure standard deviation plot ["PSDEV"] on 7/25/82 in Figure 4.18); such strong surface winds cause the regularly oscillating tidal flows to deviate substantially. Near-bottom water temperature varied little over the time scale of trap collections (e.g., see "Temperature" plot in Figure 4.18), but the water gradually cooled about 5°C from 7/27/82 to 9/22/82 (see Table 4.4).

A summary of the near-bottom water temperatures and current

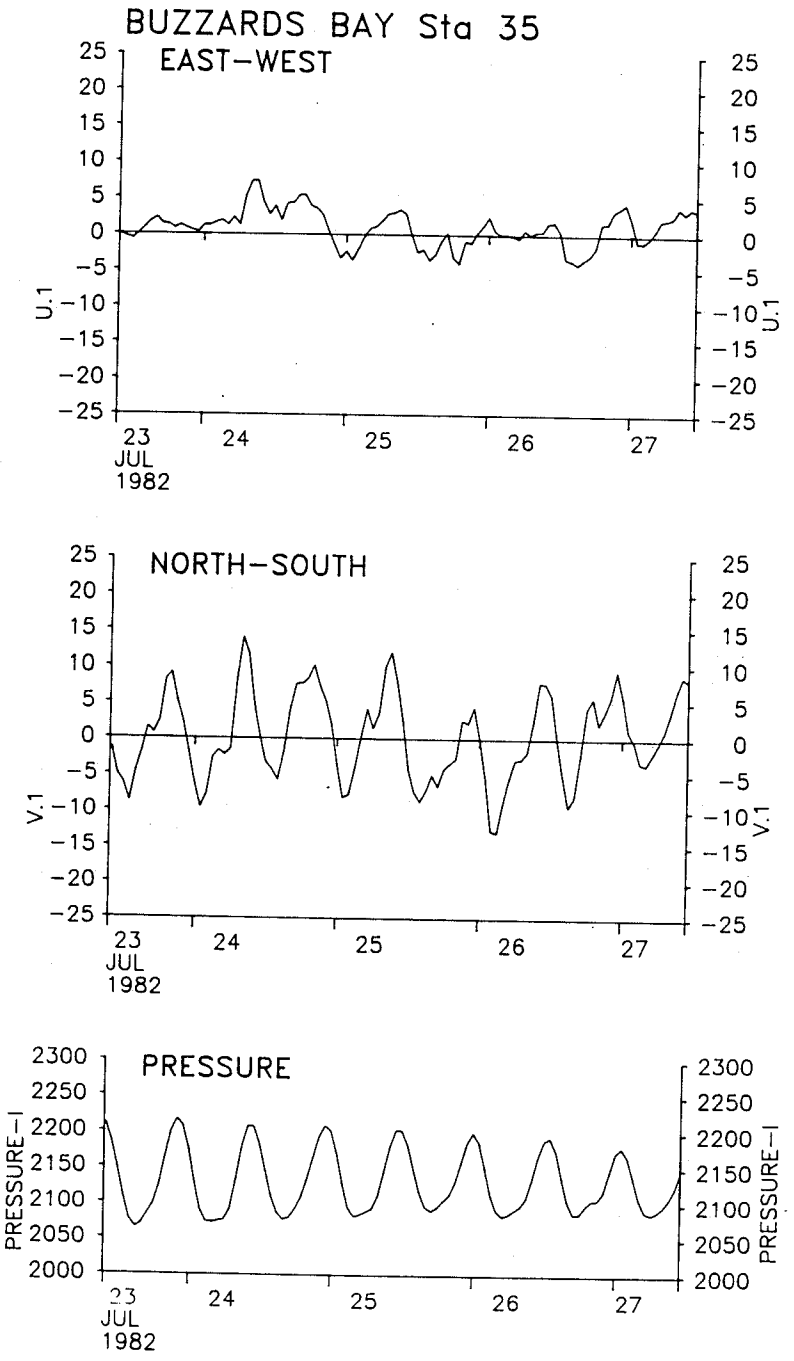

Figure 4.17: Plots of near-bottom pressure and the north-south and east-west components to the near-bottom currents at Station 35 during interval 7/27/82. The measurements were made by instruments attached to "Tripod A" (see Section 4.2.5 and location of tripod in Figure 4.5) and the values plotted are one-hour averages.

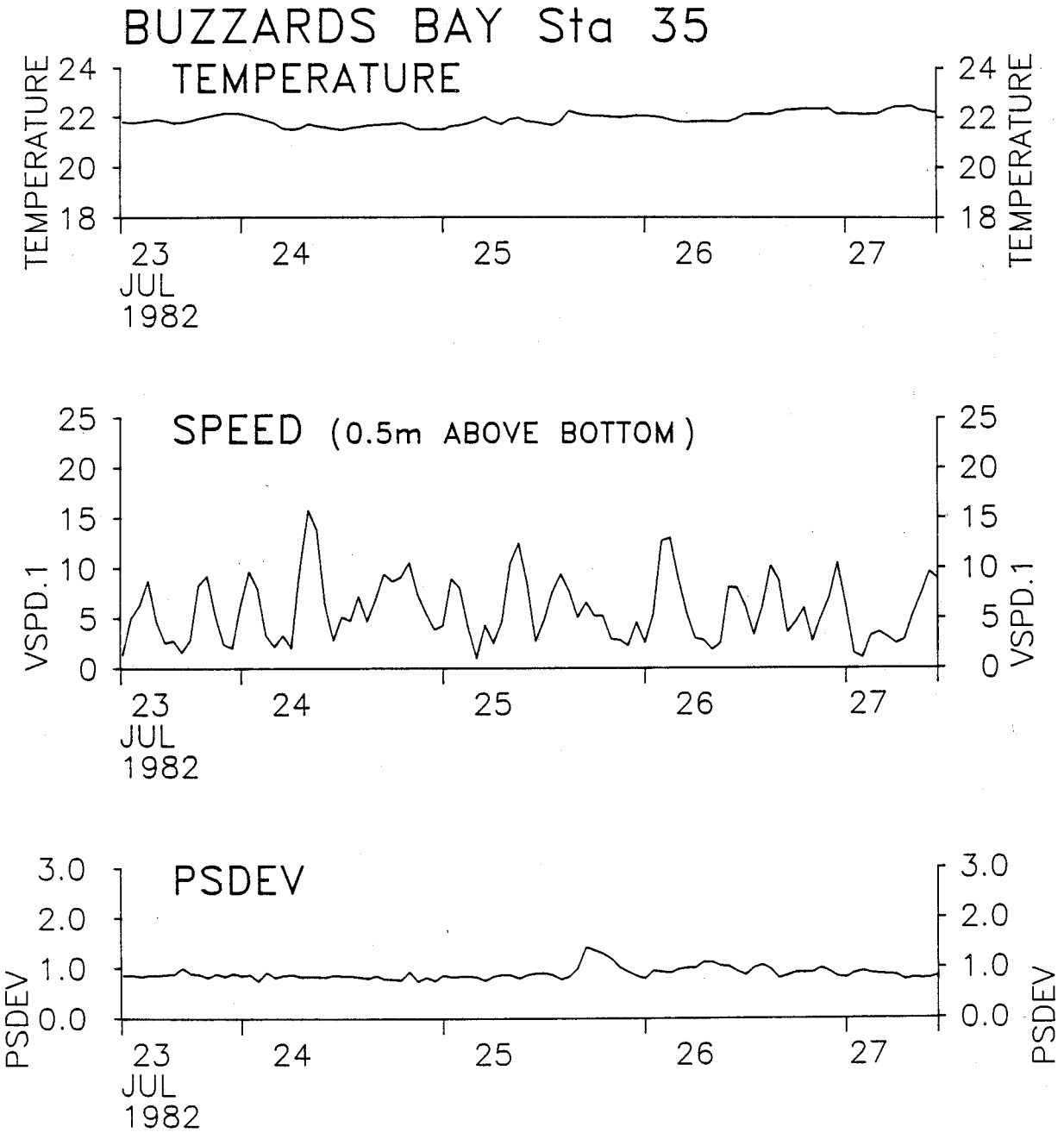

Figure 4.18: Plots of near-bottom water temperature, current speed, and pressure standard deviation ("PSDEV") at Station 35 during interval 7/27/82. The measurements were made by instruments attached to "Tripod A" (see Section 4.2.5 and location of tripod in Figure 4.5) and the values plotted are one-hour averages during the interval.

TABLE 4.4

Summary of Near-Bottom Water Temperatures and Current Speeds
During the 1982 Trap Collecting Intervals

Trap collecting interval[1]	Number of observations[2]	Near-bottom water temperature[3] Range (°C)	Mean (°C)	SD (°C)	Near-bottom current speed[4] Distance above bottom (meters)	Range (cm/sec)	Mean (cm/sec)	SD (cm/sec)
7/27/82	1569	21.3-23.0	21.9	0.3	0.5	0-20.7	5.9	3.3
8/20/82	1529	21.5-22.2	21.8	0.2	0.5	0-16.7	3.0	3.7
9/15/82	425	20.1-20.7	20.4	0.1	1.0	0-15.3	7.7	3.2
					0.5	0-15.0	5.6	2.6
9/20/82	1833	19.4-20.7	19.9	0.4	1.0	0-15.4	8.0	4.1
					0.5	0-16.7	5.4	3.8
9/21/82	345	19.1-19.6	19.4	0.1	1.0	0-14.6	5.7	3.7
					0.5	0-12.0	4.8	2.6
9/22/82	369	18.1-19.1	18.9	0.1	1.0	0-13.1	5.6	3.7
					0.5	0-10.4	3.8	2.9

1. See Table 4.1.
2. Measurements were taken every 3.75-min during the intervals (see Section 4.2.5).
3. Temperature was recorded at a distance ~ 1.5-m above the bottom.
4. The values listed here for current speeds 1.0-m above the bottom are slightly different from the values plotted in Figures 4.21 through 4.24 because the "burst" measurements (see Section 4.2.5) were used in those figures.

speeds during the 1982 trap-collecting intervals is given in Table 4.4. To further illustrate the differences in near-bottom flows among the trap-collecting intervals, histograms of current speeds during each interval are given in Figures 4.19 through 4.23.

The largest range in current speeds occurred during interval 7/27/82 (Figure 4.19 and Table 4.4), where maximum flow speeds of 20.7 cm/sec were measured 0.5-m above the bottom. The smallest range in current speeds occurred during interval 9/22/82 (Table 4.4), where maximum flow speeds of 10.4 and 13.1 cm/sec were measured 0.5- and 1.0-m above the bottom, respectively. All flow speed-frequency distributions, except one (interval 9/20/82 in Figure 4.21), are unimodal but the position of the mode differs among the intervals. The mode occurs at speeds from: 2 to 4 cm/sec for intervals 7/27/82 (Figure 4.19) and 9/22/82 (Figure 4.23), 4 to 6 cm/sec for interval 9/21/82 (Figure 4.22), and 6 to 8 cm/sec for interval 9/15/82 (Figure 4.20). The flow speeds are the most evenly distributed during interval 9/20/82 (Figure 4.21), with two slight peaks, one for flow speeds between 6 and 8 cm/sec and one for flow speeds between 12 and 14 cm/sec. The Savonins rotors, at both heights above the seabed, became so fouled with barnacle larvae during interval 8/20/82 that the current meter data could not be considered reliable for this interval.

4.4 Discussion

A brief summary of the results, by species or taxonomic group, in field tests of the a priori hypotheses concerning trap collections

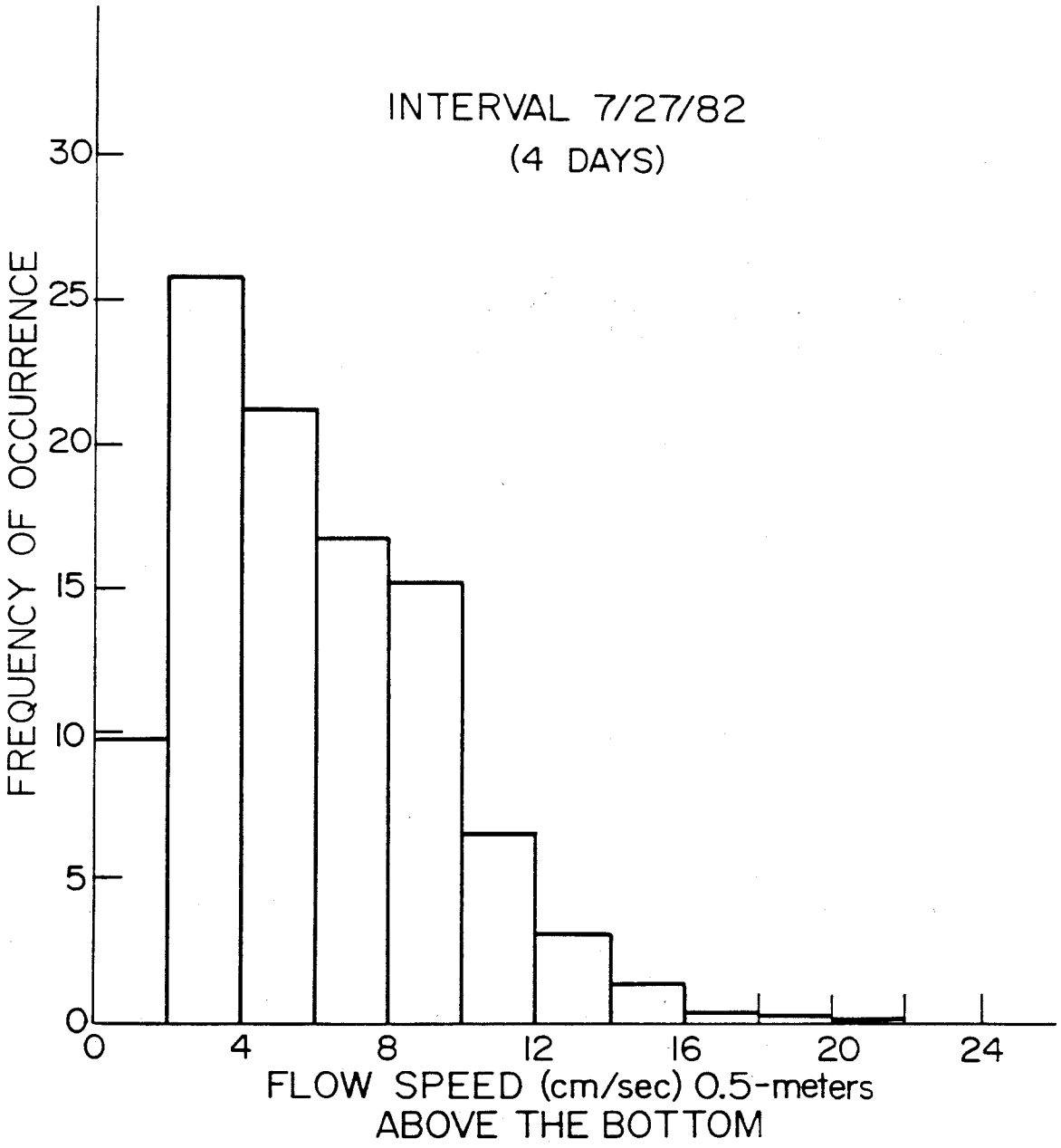

Figure 4.19: Flow speed-frequency histograms for currents measured 0.5-m above the bottom at Station 35 during interval 7/27/82. The measurements were made by instruments attached to "Tripod A" (see Section 4.2.5 and location of tripod in Figure 4.5); measurements taken at 3.75-min intervals were used for this plot.

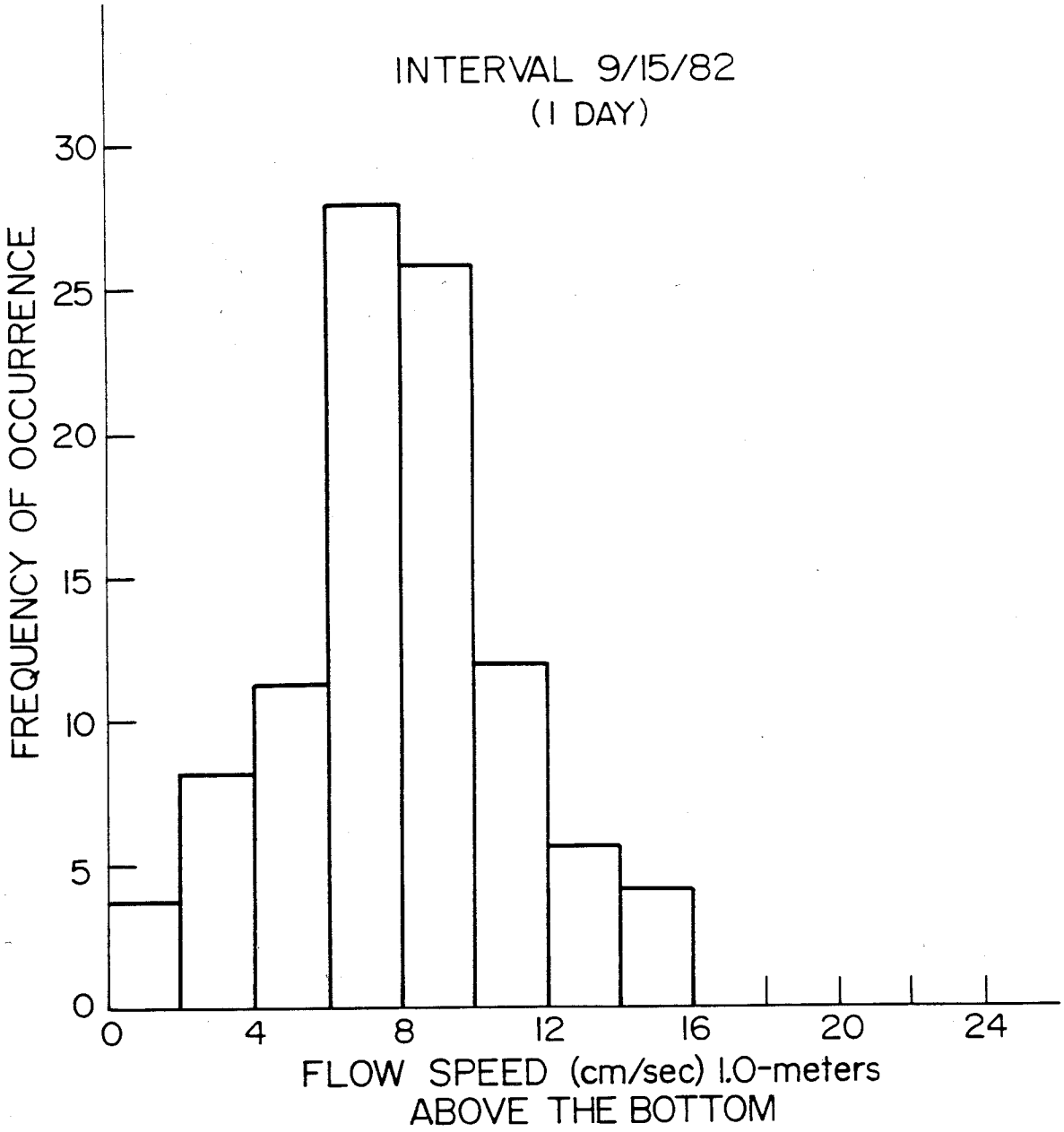

Figure 4.20: Flow speed-frequency histograms for currents measured 1.0-m above the bottom at Station 35 during interval 9/15/82. The measurements were made by instruments attached to "Tripod B" (see Section 4.2.5 and location of tripod in Figure 4.5); average values for the burst-measurements taken at the midpoint of each 3.75-min interval are plotted here.

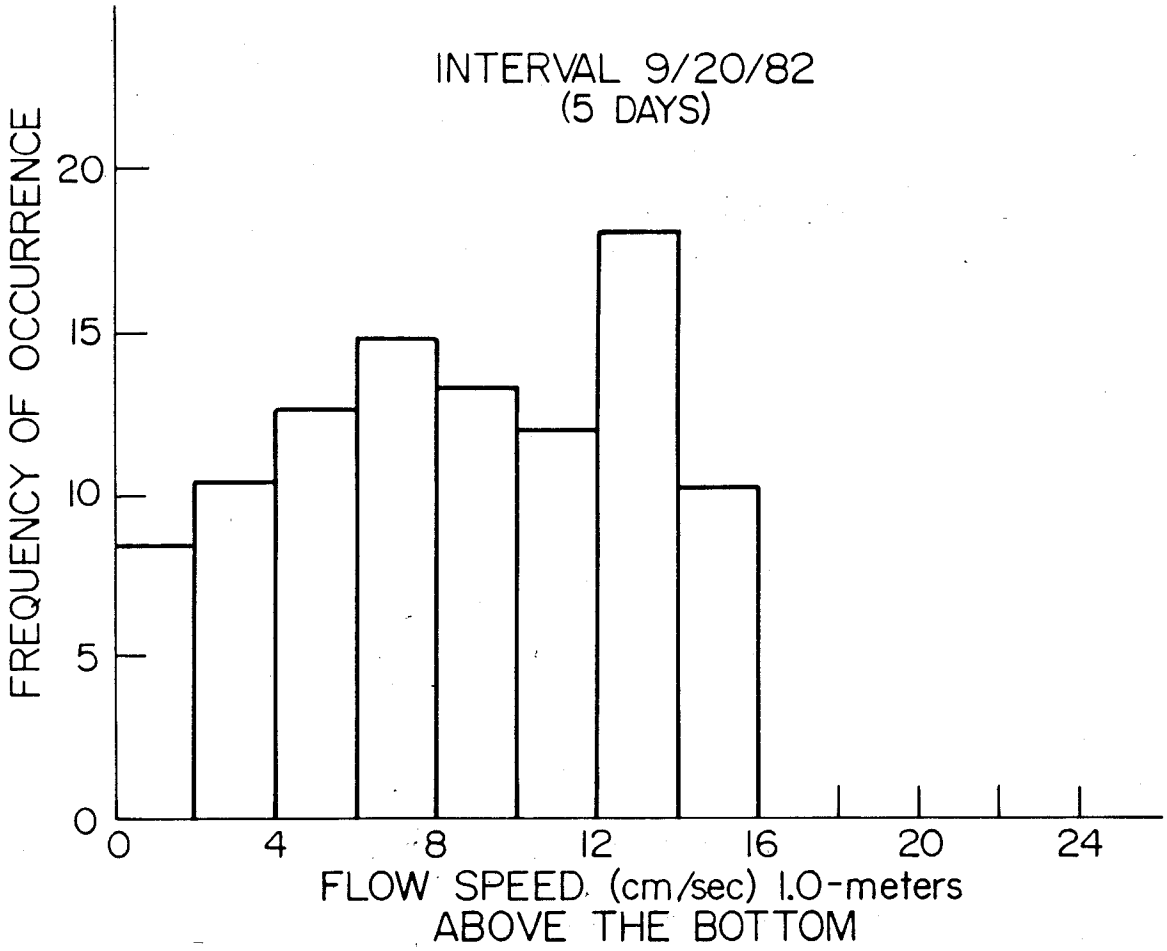

Figure 4.21: Flow speed-frequency histograms for currents measured 1.0-m above the bottom at Station 35 during interval 9/20/82. The measurements were made by instruments attached to "Tripod B" (see Section 4.2.5 and location of tripod in Figure 4.5); average values for the burst-measurements taken at the midpoint of each 3.75-min interval are plotted here.

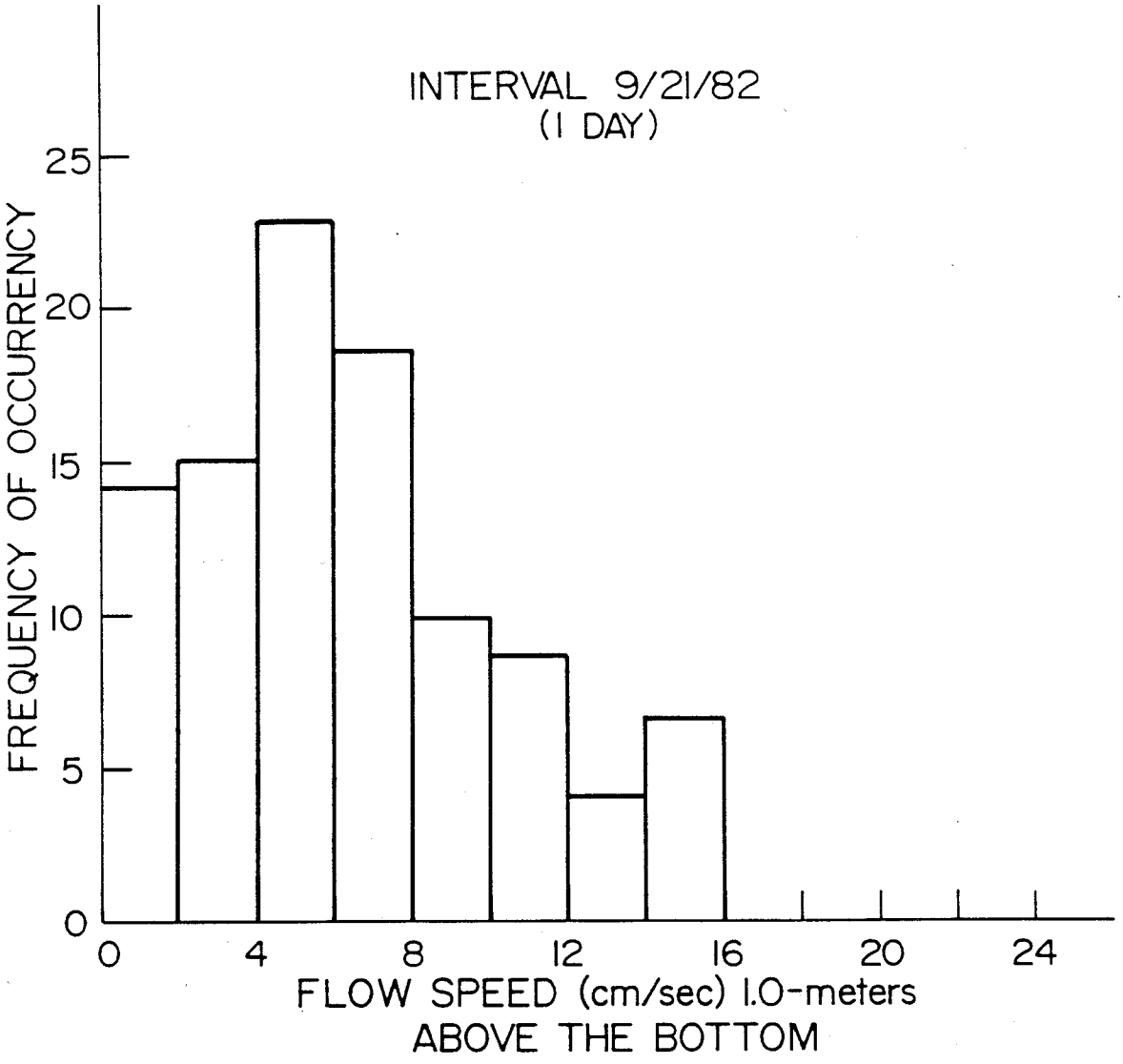

Figure 4.22: Flow speed-frequency histograms for currents measured 1.0-m above the bottom at Station 35 during interval 9/21/82. The measurements were made by instruments attached to "Tripod B" (see Section 4.2.5 and location of tripod in Figure 4.5); average values for the burst-measurements taken at the midpoint of each 3.75-min interval are plotted here.

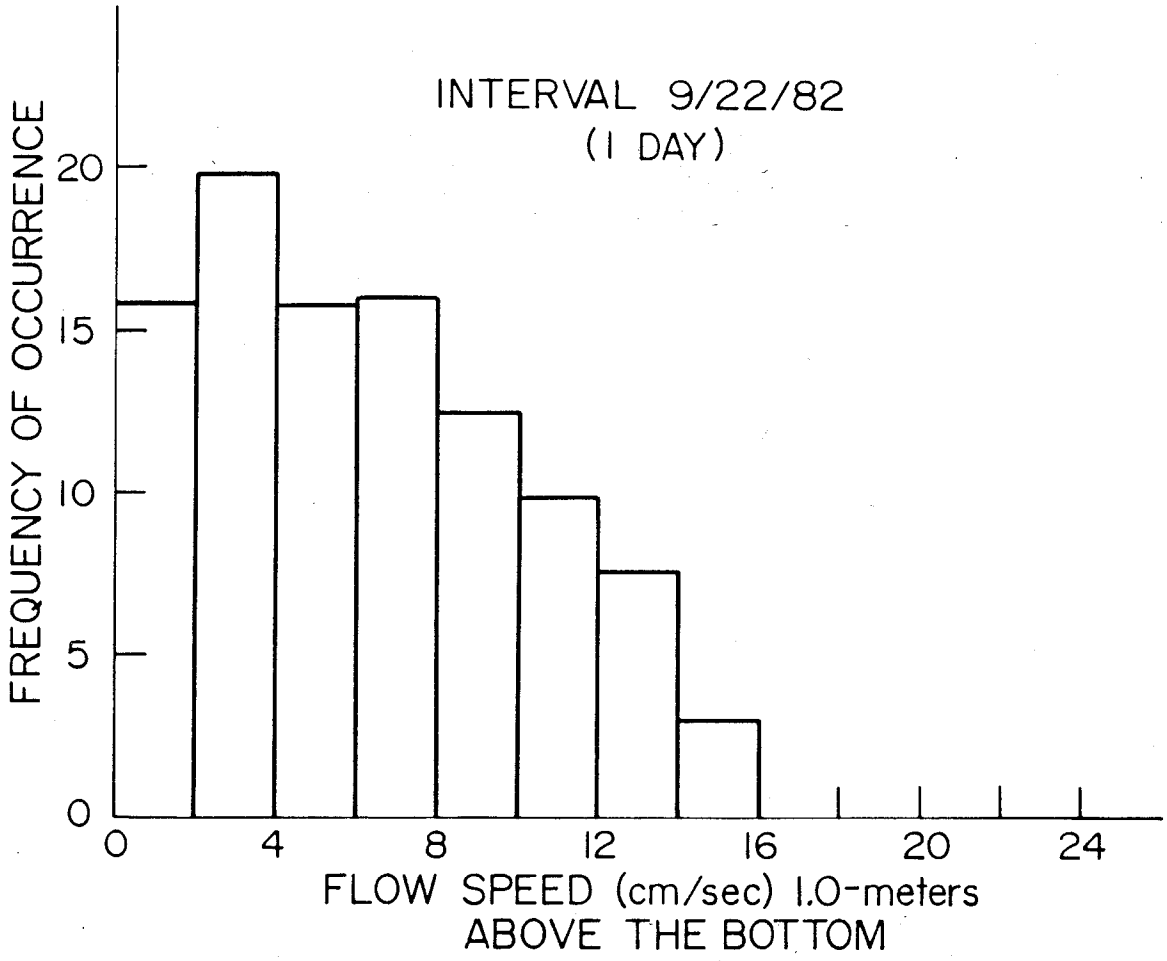

Figure 4.23: Flow speed-frequency histograms for currents measured 1.0-m above the bottom at Station 35 during interval 9/22/82. The measurements were made by instruments attached to "Tripod B" (see Section 4.2.5 and location of tripod in Figure 4.5); average values for the burst-measurements taken at the midpoint of each 3.75-min interval are plotted here.

of larvae (see Section 4.2.2) is presented first in this discussion (Section 4.4.1). Next (in Section 4.4.2), some limitations to these a priori hypotheses are discussed. Then, in Section 4.4.3, various physical, chemical and biological phenomena that may have contributed to differences in collections between intervals or between species or taxonomic group are discussed. In the last section (Section 4.4.4), the relevance of results from this study to (1) predicting settlement sites of larvae on the seabed, (2) active habitat selection by larvae, and (3) defining the appropriate spatial scales for various settlement phenomena, are discussed.

4.4.1 Tests of the a priori hypotheses regarding the collection of larvae by traps

During any given collecting interval Mediomastus ambiseta collections between trap designs corresponded to the rank order predicted for passive particle collections. All replicates of trap OPG8.3-3.0S, except two (one during interval 9/22/82 and one during interval 9/21/82, see Figures 4.8 and 4.14, respectively), collected relatively more Mediomastus per unit mouth area than replicates of trap OPC8.5-2.7S during five trap collecting intervals (see Figures 4.6, 4.8, 4.9, 4.13 and 4.14). These results support the a priori hypothesis for passive particle collections by the Group A traps (see [1] in Section 4.2.2). Collections of Mediomastus in the Group C-like traps also support the a priori predictions (see [3] in Section 4.2.2); replicate collections by traps OPC7.7-1.1S and OPC7.7-2.1S completely overlapped while collections by trap OPF8.9-2.0S were significantly less than and did not overlap with

collections by the cylinders (Figure 4.10). Collections of the postlarvae in trap TBC14.7-1.6S were usually less than collections in trap OPC8.5-2.7S and collections in the former trap design never exceeded the range in replicate collections in the latter trap design (Figures 4.12, 4.13, 4.14). These results again support the a priori hypothesis stipulated by the flume experiments for collections by these two trap designs (see [4] and [5] in Section 4.2.2). Only collections by trap OPP8.3-2.7S relative to trap OPC8.5-2.7S and by trap TBF14.7-1.6S relative to trap TBC14.7-1.6S did not fit the predictions for passive particle collections. Traps OPP8.3-2.7S and OPC8.5-2.7S collected similar numbers of Mediomastus per unit mouth area (Figure 4.9), while trap OPP8.3-2.7 was predicted to be a relative undercollector (see [2] in Section 4.2.2). Trap TBF14.7-1.6S collected more larvae than trap TBC14.7-1.6S (Figure 4.12) whereas the two trap designs did not have significantly different particle collection efficiencies in the flume (see Figure 3.34).

Collections of Pectinaria gouldii postlarvae between the various trap designs were rarely significantly different; however, the trends in relative abundances within the groups of traps tested during a given interval often support the a priori predictions (Section 4.2.2). For example, collections of Pectinaria in trap OPG8.3-3.0S were usually greater than collections in trap OPC8.5-2.7S (e.g., see Figures 4.9 and 4.14); collections in trap OPG8.3-3.0S were never less than the range in replicate collections by trap OPC8.5-2.7S (e.g., see Figures 4.6, 4.8 and 4.13).

The relative abundances of bivalve larvae and postlarvae among the various trap designs were similar to the results for Mediomastus during all intervals, except two (intervals 9/21/82 and 8/20/82), again supporting the a priori hypotheses. For interval 9/21/82, replicate collections of bivalves overlapped for all three trap designs tested, traps OPG8.3-3.0S, OPC8.5-2.7S, and TBC14.7-1.6S (Figure 4.14). Note, however, that the number of individuals collected per 55.42 cm^2 mouth area was exceedingly small (4 to 8 individuals) during this interval, compared with the other intervals, where usually 20 to 130 individuals per 55.42 cm^2 trap mouth area were collected. For interval 8/20/82, bivalve collections between the Group D trap designs fit the patterns predicted for passive particle collections (see [4] in Section 4.2.2).

Collections of sabellariid larvae in traps were similar to the bivalve collections, with one noteable exception. For the Group B traps, significantly fewer larvae were collected in trap OPP8.3-2.7S than in trap OPC8.5-2.7S (Figure 4.9), as predicted by the a priori hypothesis for passive particle collections by these trap designs (see [2] in Section 4.2.2). Collections of sabellariids among these traps are the only results supporting the a priori hypothesis for the Group B trap designs, (see [2] in Section 4.2.2).

Enteropneust postlarvae were collected only during two intervals (7/27/82 and 8/20/82, see Figures 4.6 and 4.12, respectively); in both cases the relative abundances of these organisms between or among the trap designs fit the a priori predictions.

During the one interval (8/20/82) when metamorphosing seastars

were collected, the patterns of collections among the Group D trap designs did not fit the a priori predictions (see [4] in Section 4.2.2). The funnel trap TBF14.7-1.6S collected significantly greater numbers of seastars than the cylinder, TBC14.7-1.6S (see Figure 4.12), contrary to the prediction.

In summary, trap collections of Mediomastus ambiseta postlarvae, bivalve larvae and postlarvae, enteropneust postlarvae and sabellariid larvae generally fit the patterns predicted for passive particle collections between or among the trap designs. However, the results are statistically more significant during some intervals than during others. While the rank order of collections of Pectinaria gouldii postlarvae between or among trap designs was often consistent with the a priori predictions for passive particles, the trends were rarely statistically significant. Pectinaria was usually collected in similar abundances by all trap designs tested during a given interval. For the only interval when metamorphosing seastars were collected, abundances were curiously higher in a funnel trap than in a cylinder with the same mouth diameter and height, a pattern significantly different from that predicted for passive particle collections by the two trap designs.

4.4.2 Limitations to the a priori hypotheses

In this study, falsification of the hypothesis that various trap designs collect the same relative abundances of passively sinking larvae in the field and passive particles (with fall velocities similar to larvae) in a laboratory flume, could mean one of two things: (1) mechanisms controlling larval abundances in the traps

are not solely hydrodynamical processes and biological and chemical phenomena also must be considered, or (2) trap collection characteristics in the field deviated significantly from the trap collection characteristics determined in the laboratory. The second explanation simply states that the specific a priori hypotheses regarding trap collections of passively sinking larvae (see Section 4.2.2) were not accurate because inert particles were not collected in the same relative abundances by traps deployed in the field as they were by traps tested in the flume; this constitutes a design flaw in the experiments. If a design flaw exists, then even if the a priori hypotheses cannot be rejected, the results are ambiguous (i.e., they do not necessarily imply that larvae sink like passive particles). Clearly, the success of testing the biological hypothesis central to this dissertation depends on how accurately passive particle collections in traps deployed in the field can be predicted from the laboratory flume measurements of relative particle collection efficiencies of the various trap designs.

The accuracy of the a priori hypotheses is difficult to assess. Results of the sediment trap literature review and theoretical analysis presented in Chapter Two indicate that particle collection characteristics of traps are a function of, at least, trap Reynolds number (R_t), trap aspect ratio (H/D), the ratio of the fluid velocity to the particle fall velocity (u_f/W), and trap geometry. In addition, the importance of particle-particle interactions and particle adhesion onto trap surfaces to particle collection efficiencies of traps requires experimental investigation. Because

full-scale traps were tested in the flume and deployed in the field, there is no inaccuracy in the a priori hypotheses due to differences, between environments, in trap aspect ratio or trap geometry. Possible errors associated with the other parameters is discussed below.

Laboratory experiments were designed so that values of R_t and u_f/W in the flume were within the range of the values of these parameters in the field. However, to accurately predict passive particle collections by traps in the field, flume experiments are required for the entire range of hydrodynamical conditions that occur during trap collecting intervals in the field. While near-bottom current measurements at the study site (see Table 4.4) show that flow speeds of ~ 10 cm/sec (the average flume flow speed), at the height of the trap mouth, did occur during each trap collecting interval, the tidally driven field flows are unsteady and oscillate between 0 and 15 cm/sec twice daily (e.g., see Figure 4.18). In contrast, water was circulated through the flume at a constant pumping rate so that measured flow speeds (see Table 3.9) varied by only 3 cm/sec, due only to the turbulence in the flow. Field flows also were, at least, bidirectional and were potentially multidirectional (see Figure 4.17) during some intervals, while the laboratory flow was unidirectional.

The robustness of the measured relative particle collection efficiencies in the flume study (Chapter Three), to the variability in flows that occurred during the trap collecting intervals in the field, is unknown. Trap biases in particle collection efficiencies are not expected to occur in still water (i.e., all trap designs are

expected to be accurate particle collectors) because the biases result from hydrodynamical phenomena (see Section 2.4). Thus, for the tidal flows in the field, relative differences in particle collection efficiencies between trap designs should be larger at relatively high flow speeds (at least to 10 cm/sec) and decrease to zero for still water. Because of this variability, relative differences in field collections of larvae (or inert particles) between trap designs are not expected to be quantitatively similar to the relative differences in particle collection efficiencies measured for traps in the flume. Thus, it is only appropriate to compare the rank order in collections of larvae by the various trap designs in the field to the rank order of passive particle collections by these traps in the flume. Other consequences, to larval collections in this study, of the fact that traps potentially oscillate between biased and unbiased collections in tidally driven flows, is discussed in the next Section (Section 4.4.3).

Another aspect to the flume experiments, which may contribute to inaccuracies in the a priori hypotheses, concerns the similarity between the particles used to seed the flume flow and sinking larvae collected by traps in the field. For accurate particle collection efficiencies, the flume and the field must have similar u_f/W ratios. This was attempted in this study by seeding the flume flow with spherical particles having theoretical fall velocities within the range of those measured for nonswimming polychaete larvae. Several limitations associated with this attempt to match u_f/W between the flume and the field are acknowledged below.

(1) Fall velocity measurements were made on larvae from only a small number of polychaete species (see Sections 3.2.2 and 3.2.3); all of the species, but one (Eteone longa, a phyllodocid), are in the Family Spionidae and none of the species were collected by traps during the field experiments. Species-specific differences in nonswimming larval fall velocities are unknown and must be determined in the future. The fall velocities of organisms also may vary over the course of their larval development just as, for example, the photo-response of some larvae changes during the course of their planktonic development (e.g., see Hurley 1973; Schembri 1982); such effects were not investigated here. In addition, the possible effects of and interactions between larval size, age and nutritional state on nonswimming fall velocities were not studied here and must be determined in the future. Some hypothesized differences in fall velocities between species or groups of organisms, based on results of the field study, are discussed in the next section (Section 4.4.3).

(2) Larvae had to be "narcotized to death" (see Section 3.2.2) so they would remain in a nonswimming status throughout the fall velocity measurements. The effects of the narcotizing agents and the procedures on the physiology of the organisms and the resultant effects on nonswimming fall velocity are unknown and must be experimentally investigated. However, the data available in this study (see Sections 3.3.2 and 3.4.1) suggest that errors in fall velocities, due to degradation of larval tissue following narcotizing treatments, would raise the values reported here by an order of magnitude, at the most. It is unknown whether or not particles that

vary in fall velocity by an order of magnitude are collected in significantly different relative abundances by a single trap design in a given flow regime (see Section 2.4.3).

(3) Particle concentrations in the flume were much higher than the concentration of larvae in the field; field concentrations of inert particles, with fall velocities similar to larvae, at the study site are unknown. For a given flow regime, particle aggregation is a function of particle concentration and the size and surface characteristics (i.e., chemical and electrostatic nature) of the particle (see review by McCave, in press). Clearly, the glass beads used in the flume differ significantly, in particle surface characteristics, from larvae. If trap-induced particle aggregation contributes to differences in collection efficiencies between trap designs (see Section 2.4.2), then trap collections of larvae or inert particles in the field may differ from trap collections of particles in the flume. In addition, if particle adhesion to trap surfaces is involved in the collection process (see Section 2.4.2), the different surface characteristics of glass beads and larvae may contribute to inaccuracies in the a priori hypotheses.

At this time, the degree of inaccuracy conferred by any of the above-stated differences between trap tests to determine passive particle collection efficiencies in a flume and trap deployments to collect larvae in the field cannot be assessed. The possible sources of error, outlined above, strongly suggest that results of the field experiments be critically evaluated. These limitations to the a priori hypotheses were specifically stated here to serve as

guidelines for a conservative interpretation of the results in the next section (Section 4.4.3).

The only way to adequately assess the accuracy of the a priori hypotheses is to determine the relative efficiencies for passive particle collections (of particles with fall velocities similar to the glass beads used in the flume) by the various trap designs in the field. Analyzing the sizes of particles (e.g., using a Coulter Counter) collected by various trap designs yields the necessary information only if natural suspensions consist of individual particles falling at a speed that can be predicted from their size. Because most small particles (e.g., clays) are highly aggregated in the field, this procedure was not used in the present study. What is required is an accurate method of determining the fall velocity spectrum of natural particles collected by traps.

To roughly determine if the rank order of collections for a group of trap designs was similar for passive particle collections in the flume and in the field, the sediments collected in the Group C-like traps were analyzed for the 8/25/80 collecting interval. For total weight of sediment collected by the three trap designs, the rank order of collections did not differ between the flume and the field for rack heights from 50- to 124-cm above the bed (Figure 4.15). However, at the tallest rack height, all replicate collections by Trap OPC7.7-1.1S overlapped with collections by the funnel trap, OPF8.9-2.0S, and were significantly lower than collections by trap OPC7.7-2.1S. This latter result does not support the a priori hypothesis for collections by the Group C-like trap designs (see [3]

in Section 4.2.2). Results for collections at the tallest trap heights might be explained by enhanced scour of the inside of the short cylinders (trap OPC7.7-1.1S), due to a combination of relatively higher flow speeds and relatively greater leaning (or swaying) of the PVC posts at the tall trap heights compared to the two shorter trap heights. Because the rank order of total sediment collected in the field was similar to the rank order of relative particle collection efficiencies in the flume, for the Group C-like traps at trap heights $\leq$ 124-cm above the seabed, all traps were placed below this height during the 1982 field experiments.

While total sediment varied among collections by the Group C-like trap designs, the percentage of mud in the samples did not vary significantly among the trap designs (Figure 4.16). Thus, there was no indication, among the three trap designs, that differential selection for either the sand or the mud fraction of the sediments occurred. Clearly, the bulk sediment analyses conducted here do not constitute a rigorous test of the hypothesis that collection efficiencies of the trap designs differ depending on the fall velocities of the sediment collected (see Section 2.4.3); however, the qualitative results are encouraging.

In conclusion, several possible sources of error associated with the attempts, in this study, to achieve dynamic and geometric similarily between the flume and the field for trap collections of passive particles have been outlined. Geometric similarily was achieved because the same traps were used in both environments. Dynamic similarity is probable because values of R_t and u_f/W in

the flume were within the range of values for these parameters measured in the field (except that fall velocities of the larvae actually collected in traps were not measured). However, possible errors associated with various aspects of the larval fall velocity measurements and the fact that the field flows oscillated roughly between 0 and 20 cm/sec require quantitative investigation. Thus, until error terms can be evaluated precisely, quantitatively values of the relative particle collection efficiencies of traps determined in the flume study cannot be applied directly to the field. However, the rank order of passive particle collections by the various trap designs is expected to be the sasme in the two environments. The one field test of this hypothesis (interval 8/25/80, see Figures 4.15 and 4.16) supports this contention for trap mouths at heights $\leq$ 124 cm above the seafloor. All trap mouths were placed below this height during the 1982 field experiments.

4.4.3 Variability in collections between trap designs and between trap collecting intervals: physical, chemical and biological explanations

In general, collections of Mediomastus ambiseta postlarvae, sabellariid larvae, bivalve larvae and postlarvae, and enteropneust postlarvae followed the patterns predicted for passive particle collections among the trap designs. Collections of Pectinaria gouldii postlarvae did not statistically support the a priori predictions; the postlarvae were collected in similar relative abundances by all trap designs or the trends supported the a priori predictions but were not statistically significant. Collections of

metamorphosing seastars violated the a priori predictions for two of the trap designs tested.

First in this section, alternative hypotheses to account for the observed general trends in the data are discussed. The hypotheses concern the chemical nature of the trap environments and various biological features of the larvae. Second, hypotheses are provided to account for differences in the relative collections of larvae for a pair or group of trap designs between various trap collecting intervals.

Although the observed differential collections of larvae and postlarvae between trap designs generally support the a priori hypotheses for passive particle collections, several alternative explanations are also provided here. (1) The organisms may actively select certain trap designs due to various aspects of the chemical or sedimentary environment in the trap(s). (2) Larvae may actively avoid certain trap designs, for behavioral reasons. (3) Larval predators may occur in different abundances between the trap designs so the observed larval abundances are a result of differential mortality. These three hypotheses are discussed in more detail below.

By definition, traps with relatively higher particle collection efficiencies collect more particles per unit mouth area than traps with relatively lower particle collection efficiencies. Thus, some trap designs accumulate more sediment, in the field, per unit mouth area per unit time, than others. Oliver (1979) (see also Dayton and Oliver 1980) found that the polychaete, Capitella capitata Hartman, occurred in higher abundances in "tall" cups of sediment raised above the seabed than in relatively shorter cups. He attributed this

result to active habitat selection by larvae for the "depositional" environment of the tall cups because adult populations are also higher in muddy areas compared to sandy areas. If Oliver's interpretation is correct then, for example, Mediomastus larvae may have selected trap OPG8.3-3.0S over trap OPC8.5-2.7S because the former trap design collects more particulates per unit mouth area per unit time. However, in the present study, larvae would have to perceive differences in the rate of sedimentation and respond on a time scale of less than one day (e.g., see results for Mediomastus during interval 9/15/82, Figure 4.13) because sediments were not added to traps prior to deployment and only a fine veneer of sediments, a few millimeters thick at most, collected on trap bottoms during the intervals. During one-day collections, sediments did not entirely cover the bottom surface of the traps. In addition, the bottom of traps OPG8.3-3.0S probably collected less sediment per unit bottom area than trap OPC8.5-2.7S (see Table 3.14) so if larvae respond to a particular thickness of the fine-sediment layer, then larval abundances should actually be lower in trap OPG8.3-3.0S compared to trap OPC8.5-2.7S. In Oliver's experiments the cups were initially filled with equal volumes of sediment, but the sediment surface was level with the mouth of the short cup and only about half-way up the height of the tall cup. Thus, surface sediments in the short cups could be scoured while surface sediments in the tall cups accumulated fine particles. It must be noted, too, that larvae settling onto the sediment surface in the short cups would also be subject to scour while larvae collected in the tall cups would not.

Oliver did not consider this alternative explanation for his results.

Differences between the chemical nature of sediments or the overlying water in the various trapping environments were not assessed in the present study. The bulk sediment analyses of particulates collected in the Group C-like traps during interval 8/25/80 (Figures 4.15 and 4.16) indicated that the trap designs differed in the total amount of sediment collected but not in the percentage of mud collected. If chemical reactions in sediments are quantity-dependent, the reactions may proceed differently in some trap designs than in others. It is also possible that certain trap designs do accumulate particular size fractions of particulates, on which various chemicals are bound; more detailed sediment analyses (e.g., see Whitlatch and Johnson 1974) are required to assess this possibility. For all trap designs, except traps OPF8.9-2.0S, OPF12.2-1.7S and OPF15.8-1.4S, water exchange should proceed rapidly between the trap contents and the outside flow. However, for the funnel traps, the bottom of the funnel opening was only 10 to 25 mm in diameter (see Table 4.2) and limited water exchange in the cylinder underlying a funnel was observed in the dye study (see Figure 3.40). Thus, it is possible that the water inside the funnel traps was more stagnant than the water inside cylinders; if an adverse chemical environment developed during the collecting interval, larvae may have avoided settling into the funnel trap designs or settled and died. However, no gross indications of, for example, anoxic conditions in funnel traps collected from the field were observed (see Section 4.1.1) and decomposing larvae were not

observed in these traps.

As stated in Section 4.1.1, criteria for selecting trap designs for field deployment included considerations of larval behaviors. For example, it was acknowledged that larvae may actively avoid vertical walls, so traps with relatively large mouth openings were selected for use in the field. However, all the funnel-traps present inclined surfaces that intercept the vertical path of a sinking larva. It is possible that once larvae encountered these surfaces, they actively avoided them and swam away. It is also possible that larvae actively or passively settled onto these surfaces.

Enhanced settlement of metamorphosing seastars on the funnels in trap TBF14.7-1.6S may explain the curious results that these funnel traps collected more larvae than a cylinder (trap TBC14.7-1.6S), with the same mouth diameter and height (see Figure 4.12). Metamorphosing seastars have morphological adaptations (e.g., a sucker) for attachment to a surface that the other larvae collected in this study do not possess. Thus, the relatively high seastar abundances in the funnel traps may have been due to the greater surface area for attachment. The larvae may actively seek such attachment surfaces or, following passive deposition onto the funnel surface, the seastar larvae may be retained better (i.e., resist scour or resuspension) because of their attachment capabilities. While this mechanism initially increases the relative abundances of seastars in the funnel traps, the seastars must eventually go through the bottom of the funnel (either actively or passively), because the funnels were removed from the traps prior to capping in the field. In addition,

Mediomastus abundances in this funnel trap design also tended to be higher than in the cylinder (see Figure 4.12). It is possible that Mediomastus larvae are stickier than the other larvae collected in this study so Mediomastus abundances are also enhanced on the funnel surface.

The dimensions of the trap designs deployed in 1982 were also selected to allow larvae equivalent vertical distances for sinking or swimming inside all trap designs (see Section 4.1.1). However, five of the designs, traps OPG8.3-3.0S, TBF14.7-1.6S, OPF8.9-2.0S, OPF12.1-1.7S and OPF15.8-1.4S have inclined surfaces surrounding the mouth, that a swimming larvae might bump into during its upward descent. Thus, for a portion of the trap mouth area, larvae may be unable to escape from these trap designs. However, collections by trap OPG8.3-3.0S were compared with collections by trap OPC8.5-2.7S, having a similar mouth area, so it is expected that an equivalent number of individuals could actively enter or leave the mouths of these two trap designs. In addition, the bottom funnel openings of trap TBF14.7-1.6S is similar to the mouth opening of trap OPC8.5-2.7S, also deployed during the 8/20/82 collecting interval (see Figure 4.12). If collections by the former trap design are normalized to this funnel area, rather than to the trap mouth area, the trap is a relative overcollector. However, equivalent numbers of larvae also should be allowed to actively enter and leave the bottom of the funnel in trap TBF14.7-1.6S and the mouth opening of trap OPC8.5-2.7S.

The only evidence of a predation effect inside any of the traps

was during interval 7/27/82, when juvenile cunners were collected in most of the trap designs (see Figure 4.7). Abundances of Mediomastus and bivalves in both trap designs deployed during this interval were negatively correlated (r_s = - 0.91 and -0.90, respectively) with the number of fish per trap. In addition, more fish were collected in replicates of trap OPC8.5-2.7S than in replicates of trap OPG8.3-3.0S; larval abundances were also lower in the former trap design. However, the predation effect alone cannot account for the approximately two-fold difference in larval collections between the trap designs (see Figure 4.6) because each fish may have eaten only about five Mediomastus larvae during the collecting interval (see Figure 4.7) and replicates of trap OPC8.5-2.7S and OPG8.3-3.0S, each containing only one fish still differed in their Mediomastus collections by a factor of ~ 1.6 (Figure 4.7). The possibility that fish or other larval predators periodically entered some trap designs and exited the traps before they were retrieved from the field, cannot be discounted.

In summary, the alternative explanations for the observed general trends in larval collections that support the a priori hypotheses must be investigated in more detail in the future. Evidence supporting any of these hypotheses is not strong, at this time. In addition, the various effects may explain differences in collections between some, but not all of the trap designs. Results of the seven field experiments are convincing support for the passive sinking hypothesis because, for all groups of trap designs tested, the abundances of from one to five of the species or groups fit the

patterns predicted for passive particle collections.

Several interesting results, which do not appear to support the passive sinking a priori hypotheses, are now discussed. Collections of Pectinaria among the trap designs usually were not statistically different, although Pectinaria postlarvae tended to be collected in the general patterns predicted for passive particle collections. Generally Pectinaria postlarvae were more evenly distributed among all trap designs than any other organism. This genus may differ from the other polychaetes collected because it may build a parchment-like tube while still in the water column, as reported for another Pectinaria species (Lacall 1980). Most Pectinaria found in the traps were inside these tubes and empty tubes were always found in samples with tubeless Pectinaria. It is suggested here that, once planktonic Pectinaria secrete the tube, their fall velocities substantially increase and they fall toward the seabed like sands. Hydrodynamical processes that result in biased trapping are less effective for a certain class of heavy particles than for relatively light particles because, for a hydrodynamically specified range of particle fall velocities, the heavier particles are not retained in the turbulent eddies shed into the trap mouth (see Section 2.4.2). Thus, for some range of particle fall velocities, traps would not act as biased collectors; hydrodynamically, trap collections of these relatively heavy particles approach the no flow condition so the particles are collected by the different trap designs in equivalent numbers per unit mouth area. It is hypothesized here that metamorphosed Pectinaria, which have secreted tubes while in the water column, are

in this class of particles. This hypothesis is easily testable in the future by measuring fall velocities of Pectinaria and conducting flume experiments using particles with similar fall velocities.

Collections of organisms by trap OPP8.3-2.7S did not support the a priori hypothesis for collections by the Group B traps (see [2] in Section 4.2.2), except for collections of sabellariid larvae. It is possible that this plate-trap design may not undercollect particles in the field in the same way that it undercollects particles in the flume. The unidirectional flow in the flume slowed as it moved over the plate so that the particles which fell onto the plate surface could not be resuspended and transported away (see Section 3.3.6 and Figure 3.41); thus, these particles did not fall through the mouth opening. However, the variable flow speeds and bi- and/or multi-directional nature of the field flows may resuspend or just move these particles around so they do fall through the trap mouth. If this was so, the plate trap in the field would be expected to have a particle collection efficiency similar to a cylinder with the same mouth diameter, trap OPC8.5-2.7S. The larvae results for Mediomastus, Pectinaria and bivalves support this explanation. It is curious, however, that sabellariid larvae were relatively undercollected by this trap design while the other groups were not.

An explanation for variability in the magnitude of differences in larval collections between the same group of trap designs deployed during more than one collecting interval is now provided. As previously discussed (Section 4.4.2), traps are biased collectors only in moving fluid and, because the flows at the study site are

tidally driven, periods of no flow or low flow usually occur twice daily (e.g., see Figure 4.18). Assuming constant larval availability, it is suggested here that there are larger differences in larval collections between trap designs for collection intervals with relatively strong flows. Thus, for example, the largest range in flow speeds occurred during interval 7/27/82 while the smallest range in flow speeds occurred during interval 9/22/82 (see Table 4.4); results were highly significant (the H_0 was rejected at $p \leq 0.014$) for differences in Mediomastus and bivalve collections between the Group A traps during interval 7/27/82 (Figure 4.6) and only moderately significant ($p < 0.100$) for interval 9/22/82 (Figure 4.8). Also, during interval 9/15/82, flow speeds from 6-10 cm/sec occurred 54 percent of the time (Figure 4.20) and during interval 9/21/82 flow speeds within this range occurred only 28 percent of the time (Figure 4.22); differential collections of Mediomastus, bivalves and sabellariids were, again, more significant during the interval with a higher percentage of stronger flows (compare Figures 4.13 and 4.14). The effects of variability in larval availability over the tidal cycle or between collecting intervals must also be considered; however, accurate data on larval availability are difficult, if not impossible, to obtain at this time (see Hannan 1981).

4.4.4 Relationship of these results to the passive deposition and active habitat selection hypotheses for larval settlement onto the seabed

The hypothesis that larvae sinking toward the seabed in the field and passive particles sinking in a flume are collected in

similar relative abundances by near-bottom traps could not be falsified in an overwhelming majority of the field experiments performed in this study. While this result strongly suggests that larvae sink through near-bottom waters like passive particles, the possibility cannot be discounted that some other process(es) (e.g., biological) could have produced the observed patterns of larval collections in the traps. As previously stated (see Section 4.1.1), an explicit result, at a given probability level, accompanies only the falsification of a hypothesis. For example, the explicit result of falsifying the passive sinking hypothesis tested in the present study is that, at the specified probability level, passive physical processes do not determine collections of larvae by near-bottom traps. However, because the hypothesis generally was not falsified in this study, passive physical processes could have produced the patterns of larval collections observed in the traps. In fact, an implicit result of this study is that considerations of hydrodynamical processes must be included in any future studies of processes that determine patterns of larval settlement. The passive sinking hypothesis should be used as an alternative hypothesis against which other (e.g., biological) hypotheses can be tested.

Results from this study indicate that the abundant larvae collected in traps deployed at the study site may sink like passive particles, at least down to heights of ~ 50-cm above the seabed. The results further suggest that the larvae respond to small-scale fluid flows and turbulence like passive particles (because these small-scale hydrodynamical phenomena are involved in the process of biased

biased collections of particles by various trap designs); thus, larvae may initially reach the seafloor where particulates, with fall velocities similar to larvae, initially settle. The range of fall velocities measured for nonswimming larvae in this study corresponds primarily to fall velocities for the upper-range of natural silt particles (see Figure 3.16) in the ocean. However, attempts to determine if larval or adult distributions correlate with the percentage of silts in field sediments are here discouraged, for two reasons. First, larvae could be deposited on the seabed during depositional events, even in sandy areas. Once deposited, the larvae may burrow into the sediments to avoid resuspension. Second, differential post-settlement mortality may obscure patterns of initial settlement in the field.

The abundances of Mediomastus postlarvae in traps placed 50- to 185-cm above the seafloor (see Figure 4.10) suggested an inverse relationship between the number of larvae collected per trap and the height of the trap mouth above the seafloor. Thus, larvae may be concentrated in near-bottom waters (e.g., see Wilson 1982). Alternatively, the results may indicate that newly settled larvae are easily resuspended from the seafloor because the total amount of sediment collected in these traps (see Figure 4.15) was also inversely related to the height of the trap mouth above the bed.

The results presented here suggest that larvae could be passively deposited onto the seabed at the same spatial scales that apply to sediment transport and deposition. Variability in larval collections for replicate traps, separated by up to 30 m, was

normally very low (e.g., see Figures 4.3 and 4.10) suggesting that larvae may be passively deposited on spatial scales of at least tens of meters.

While larvae may initially reach the seafloor like passive particles, the larvae may not necessarily remain at the deposited locale. Several options are possible. (1) Larvae or postlarvae may actively choose microenvironments within a given location (see active habitat selection references reviewed in Sections 1.2.4 and 1.2.5) by crawling or swimming along the bottom. (2) Larvae may voluntarily leave the area by actively swimming above the sediment surface or by simply remaining on the surface to be resuspended and transported away (e.g., see Bell and Sherman 1980; Palmer and Brandt 1981; also, Doyle [1975, 1976] suggested that larvae may select settlement sites by actively rejecting areas that do not provide a required threshold stimulus perceived by the larva as it travels downstream). (3) Larvae may be redistributed only during storm events when usually the top 2 cm of the sediment surface and the organisms contained in these sediments can be resuspended and transported (e.g., see Hogue 1982; Dobbs and Vozark 1983). (4) Larvae may be redistributed as passive accumulations around microtopographic features (e.g., see Eckman 1979, 1983; Hogue and Miller 1982). An alternative to these hypothesized redistribution mechanisms is that larvae may be deposited over a relatively large area of the seafloor and differentially survive in the most suitable habitats.

Further studies are required to test the ideas outlined here.

This research serves as a first step toward understanding the role of hydrodynamical processes in determining larval settlement patterns in the field. More observational and experimental work is needed on larval biology and ecology during settlement to form hypotheses against which the passive deposition hypothesis can be tested.

4.5 Summary

The hypothesis that larvae sinking toward the seabed in the field and passive particles (with fall velocities similar to larvae) sinking in a flume are collected in similar relative abundances by near-bottom traps was tested using eight different trap designs deployed, in groups of two or three, during seven separate collecting intervals. The rank order that trap designs within a group (deployed simultaneously in the field) should collect larvae, if larvae sink like passive particles, was stipulated from the flume experiments (Chapter Three). The traps were not expected to collect larvae at same relative collection efficiencies that the traps collected particles in the flume because the field environment could not be mimicked exactly in the flume. Physical measurements, during trap collections, using a bottom-moored tripod system did indicate that near-bottom flow speeds in the field oscillated roughly between 0 and 20 cm/sec on a semidiurnal tidal cycle so the 10 cm/sec flow used in the flume was within the range of the field flow speeds.

Trap collections of Mediomastus ambiseta postlarvae, bivalve larvae and postlarvae, enteropneust postlarvae and sabellariid larvae generally fit the patterns predicted for passive particle collections

between or among the trap designs. However, the results are statistically more significant during some intervals than during others. Differences between intervals in the intensity and/or duration of flow speeds required for biased trapping (i.e., traps are not biased collectors in still water) and in larval availability is a plausible explanation for differences in biased trap collections between intervals. In fact, near-bottom flow speed measurements during the collection intervals are consistent with this explanation.

Collections of Pectinaria gouldii postlarvae between or among trap designs was often consistent with a priori predictions for passive particle collections, but the trends were rarely statistically significant. Pectinaria was usually collected in similar abundances by all trap designs tested during a given interval. Because Pectinaria may secrete a larval tube structure while it is still in the water column and the vast majority of Pectinaria collected in the traps were inside these tubes, it is hypothesized that settling Pectinaria are relatively heavy larvae (compared to the tubeless spionids measured in this study) and have fall velocities within the range of the relatively heavy particles that are not differentially collected by traps. Thus, Pectinaria may also be collected like passive particles.

Metamorphosing seastars were collected only during one interval and abundances were curiously higher in a funnel trap than in a cylinder with the same mouth diameter and height, a pattern significantly different from that predicted for passive particle collections by the two trap designs. The metamorphosing seastars

have a sucker for attachment to a surface during metamorphosis. Enhanced abundances of these larvae in the funnel traps may have resulted from the greater surface area for attachment provided by the funnels. However, because the funnels were removed from the traps before capping in the field the attached seastars eventually must be swept through the bottom funnel opening for this explanation to be valid.

The following three alternative explanations for the observed larval collections among the trap designs were discussed. (1) The organisms actively select certain trap designs due to various aspects of the chemical or sedimentary environment in the trap(s). (2) Larval actively avoid certain trap designs, for behavioral reasons. (3) Larval predators occur in different abundances between the trap designs and effect differential larval mortality. Evidence supporting any of these alternative explanations is not strong, but these hypotheses require rigorous testing in the future.

The fact that the passive sinking hypothesis could not be falsified in most of the field experiments conducted here implies that hydrodynamical processes must be included in any future studies of processes that determine patterns of larval settlement. However, passive sinking by larvae is not the explicit result of this experimental study. Other processes that could have produced the observed patterns of larval collections among trap designs now must be tested against the passive sinking alternative hypothesis.

If larvae sink like passive particles to heights of ~ 50-cm above the seabed, as the results of this study suggest, then it is

possible that larvae initially reach the seafloor at sites where particulates, with fall velocities similar to larvae, initially settle. This hypothesis must be tested experimentally. However, the larvae may not remain at these initial settlement sites, but they could actively choose microenvironments within a given location, they may be resuspended and transported regularly or during storm events, and/or they may passively accumulate at smaller spatial scales around microtopographic structures. Alternatively, larvae may be passively deposited over relatively large areas (i.e., at the spatial scales that apply to fine sediment transport and deposition) and differentially survive in certain habitats.

5. SUMMARY AND CONCLUSIONS

This dissertation research was stimulated by a void in the larval ecology literature of studies that experimentally investigated the relationship between small-scale ($\leq$ tens of meters) hydrodynamical processes and patterns of initial larval settlement. While large-scale ($\geq$ tens of kilometers) larval dispersal has been assumed primarily a passive process controlled by general oceanic circulation, larval settlement at very small spatial scales ($\leq$ centimeters) has been presumed primarily an active process where larvae choose the substrate most suitable for settlement. However, the spatial scales (millimeters to tens of meters) over which active larval choice has been demonstrated are one to three orders of magnitude smaller than the spatial scales (tens of meters to kilometers) over which patterns of species and sediment distributions have been observed in the field.

A mechanism to account for patterns of initial larvae settlement must operate at the relatively large spatial scales that apply to sediment transport and deposition while allowing active larval choice to operate at much smaller spatial scales. Passive deposition of larvae onto the seabed at sites where particulates (with fall velocities similar to larvae) initially settle is one such mechanism. Once initially deposited, however, the larvae may redistribute at smaller spatial scales (i.e., via active habitat selection, as observed in a plethora of very small-scale laboratory studies).

The hypothesis that larvae sink through turbulent near-bottom waters like passive particles was experimentally tested in this study. Due to

complex biological and physical processes occurring once larvae have settled on the bottom, the passive deposition hypothesis cannot be tested by directly sampling the seabed for initially deposited larvae and inert particles. Thus, the present study was initiated to determine if larvae, that are capable of settlement, act like passive particles while they are falling toward the seabed in typical turbulent near-bottom flows. Determining if larvae sink like passive particles in flows near the seafloor is a necessary prerequisite to testing the passive deposition hypothesis. If the passive sinking hypothesis cannot be falsified, then considerations of passive physical processes must be included in all future studies of larval settlement phenomena.

The experimental approach in the present study involved using the biased sampling characteristics of sediment traps to collect particles and larvae falling toward the sediment surface. Traps differentially collect sediments because of self-induced local disturbances to the flow field; this effect is dependent upon trap geometry so that traps of various shapes will collect passive particles in different relative abundances. By differentially collecting particles, the traps simulate some of the small-scale hydrodynamical processes responsible for transporting and depositing sediments on the seabed. If larvae act like passive particles in these near-bottom flows, then larvae and particles (with fall velocities similar to larvae) should be collected in the same relative abundances by the traps. If larvae are not collected according to the patterns predicted for passive particles, then other processes (e.g., biological features of the larvae such as behaviors or physiological responses) are governing the falling of larvae through

near-bottom waters and the collection of larvae by traps.

This research consisted of three basic research components: (1) a theoretical analysis of the hydrodynamical processes governing particle collection by sediment traps in near-bottom turbulent flows, (2) a laboratory study to measure fall velocities of nonswimming polychaete larvae and to determine the particle collection efficiencies of various trap designs in a flume, and (3) a field study to experimentally test the passive sinking hypothesis by deploying a variety of trap designs, stipulated from the flume study, to collect larvae near the bottom in a shallow subtidal turbulent flow environment. Results of these three aspects to this research are summarized below.

Results of the dimensional analysis of the variables relevant to the process of trapping particulates indicated that particle collection efficiency should be a function of primarily three dimensionless parameters (trap Reynolds number, trap aspect ratio, and the ratio of the fluid velocity at the height of the trap mouth to the particle fall velocity) and of trap geometry. The dimensional analysis indicated only that a relationship between collection efficiency and the parameters may exist, for some range of conditions. A dimensional analysis does not indicate the nature of the dependence. Thus, for a first approximation of how the dimensionless parameters may quantitatively effect particle collection efficiency, results from the five published laboratory studies (Peck 1972; Tauber 1974; Gardner 1980a; Hargrave and Burns 1979; Lau 1979) that investigated trap collection characteristics were summarized, relative to the dimensionless parameters.

From this literature review of observed trap biases, three hypotheses

were developed regarding biased particle collections by cylinders and two hypotheses were developed regarding the relationship of collection efficiency to trap geometry. The hypotheses are stated below. (1) Particle collection efficiency should decrease over some range of increasing trap Reynolds number. (2) Particle collection efficiency should decrease over some range of decreasing particle fall velocity. (3) At a given trap Reynolds number, particle collection efficiency should increase over some range of increasing trap aspect ratio. (4) Relative to a cylinder, small-mouth wide-body traps (having the same mouth diameter as the cylinder) should have higher collection efficiencies. (5) Relative to a cylinder, funnel traps (having the same mouth diameter as the cylinder) should have lower collection efficiencies.

Theoretical arguments or models were provided to explain these hypothesized effects. The models require experimental testing. The hypothesized biased trapping effects were provided as an aide for future studies of traps. Experiments might be fruitfully organized if they are aimed at testing these hypotheses. In fact, a test of the first hypothesis was conducted in the present study (see Appendix II) and the hypothesis could not be falsified.

From the theoretical analysis it is clear that characteristics of particle collecting traps require rigorous investigation in the future. The laboratory studies, to date, provide a valuable groundwork for future experiments but must be evaluated in light of their limitations. It is further emphasized that laboratory experiments must be carefully designed so that, (1) competing physical effects are minimized (i.e., trap Reynolds number must be held constant when aspect ratio effects are being tested

and visa versa), and (2) dynamic and geometric similarity to the field is achieved (i.e., trap Reynolds number and particle characteristics, especially particle fall velocity, must be matched).

The theoretical analysis stipulated that traps must be flume-tested for the particular hydrodynamical conditions of interest in this study. That is, in the flume, traps must collect particles having fall velocities similar to larvae and the flume flow regime must be dynamically similar to the field flow regime. Thus, fall velocities of larvae were measured in the laboratory prior to the flume experiments.

Nonswimming fall velocities were measured on planktonic larvae of several polychaete species (Eteone longa, Streblospio benedicti, and other spionid species). The larvae were anesthetized and then introduced into a temperature-controlled column of seawater, where fall velocity measurements were made. Calibrations of the techniques using spheres indicated that the imprecision in the fall velocity measurements was about 10 percent. For larvae ranging from 300 to 1400 μm in narcotized length, fall velocities (normalized for 30 ppt salinity, 20.4°C seawater) ranged from 0.0129 to 0.374 cm/sec. Fall velocity was positively correlated with narcotized length. The larval fall velocities are equivalent to the theoretical fall velocities (normalized to the same seawater conditions) of spherical quartz particles ranging from 16 to 70 μm in diameter. Thus, the nonswimming polychaete larvae tested fall primarily like silt particles (quartz particles ranging from 3.9 to 62.5 μm in diameter) in the ocean. Based on the larval fall velocity measurements, two mixtures of spherical glass beads were selected to seed the flume flow: theoretical fall velocities (in 24°C freshwater) ranged

from 0.014 to 0.32 cm/sec for ~ 97 percent of the 25-μm bead mixture and theoretical fall velocities (in 24°C freshwater) ranged from 0.081 to 0.42 cm/sec for ~ 94 percent of the 46-μm bead mixture.

The particle collection efficiencies of sixteen different trap geometries, as well as screened and baffled versions of some of these traps, were tested in a freshwater laboratory flume during five series of experiments. The flow was continuously seeded with the bead mixtures indicated above and the flow speed was about 10 cm/sec, within the range of flow speeds measured 1.0-m above the bottom at the field study site. Flume experiments were carefully designed according to criteria for achieving dynamic and geometric similarity to field conditions.

Only relative particle collection efficiencies were calculated for the traps tested in this study; all collection efficiencies were normalized by the mean particle collection efficiency of a cylindrical trap that was tested during each series. This trap design was also used in nearly all of the field experiments. Calculated total measurement error for the techniques used in this study indicated that an average of ~ 10 percent imprecision could be expected for replicate tests of the same trap design. The average measured between-replicate variability was ~ 16 percent, but varied between 0.1 and 42 percent. Thus, trap designs were considered biased collectors, with respect to each other, only if their particle collection efficiencies differed by 20 percent, or by the combined coefficient of variation for the two trap designs, whichever value was largest.

Based on results of the flume study, four groups of traps were selected for deployment in the field. Specific a priori hypotheses were

stated regarding the rank order of particle collections by the trap designs within each group. Collections of larvae by the traps within each group then could be compared to the a priori predictions, to test the null hypothesis that larvae and passive particles are similarly collected by the traps.

Several hydrodynamic hypotheses also were presented to explain the biased trapping of particles by some of the trap designs tested in this study. The hypotheses were based on results of the qualitative dye study of flow near and inside the mouths of several trap designs, on the quantitative results and on the theoretical analysis present in this study. The hypotheses remain to be experimentally tested. The results of this flume study suggest that the collection characteristics of traps must be researched in much more detail before reliable measurements of particulate flux can be made with any trap design.

The hypothesis that larvae sinking toward the seabed in the field and passive particles (with fall velocities similar to larvae) sinking in a flume are collected in similar relative abundances by near-bottom traps was tested using eight different trap designs deployed, in groups of two or three, during seven separate collecting intervals. The rank order that trap designs within a group (deployed simultaneously in the field) should collect larvae, if larvae sink like passive particles, was stipulated from the flume experiments (Chapter Three); however, the traps were not expected to have the same relative larval collection efficiencies as determined for particles in the flume because the field environment could not be mimicked exactly in the flume. The field experiments were conducted in a shallow (15 m depth) subtidal region of Buzzards Bay, MA,

where semidiurnal tidal flows oscillated between 0 and 20 cm/sec.

Trap collections of Mediomastus ambiseta (a polychaete worm) postlarvae, total bivalve larvae and postlarvae, sabellariid polychaete larvae and enteropneust postlarvae generally fit the patterns predicted for passive particle collections between or among the trap designs. While the results were statistically more significant during some intervals than during others, the rank order of larval collections by each group of trap designs nearly always corresponded precisely to the rank order of passive particle collections in the flume experiments. Thus, the hypothesis that larvae sinking toward the seabed in the field and passive particles (with fall velocities similar to larvae) sinking in a flume are collected in the same rank order of abundances by near-bottom traps could not be falsified for collections of organisms from three invertebrate phyla.

Collections of the polychaete, Pectinaria gouldii, between or among trap designs were often consistent with the a priori predictions for passive particle collections, but the trends were rarely statistically significant. Pectinaria was usually collected in similar abundances by all trap designs tested during a given interval. Pectinaria postlarvae collected, even during one-day intervals, were usually found inside a larval tube structure; presumably these tubes were secreted while the organisms were still in the water column, as reported in the literature for another Pectinaria series. Thus, it was hypothesized that the fall velocities of metamorphosed Pectinaria in tubes are significantly greater than the fall velocities of the spionid larvae measured in this study. A certain range of fast-falling inert particles is expected to be

unaffected by the hydrodynamical processes responsible for trap biases, and it was further hypothesized that the Pectinaria postlarvae have fall velocities within this range. Because the fast-falling particles would be collected in similar abundances by all trap designs, trap collections of Pectinaria may also fit the patterns predicted for passive particle collections by traps.

Metamorphosing seastars were collected only during one interval and abundances were significantly higher in a funnel trap than in a cylinder with the same mouth diameter and height, contrary to the a priori predictions for passive particle collections by these two trap designs. The seastars collected were usually in the brachiolaria larval stage, possessing the characteristic brachiolar arms and sucker for attachment to a surface during metamorphosis. Enhanced abundances of these larvae in the funnel traps may have resulted from the greater surface area for attachment provided by the funnels. However, because the funnels were removed from the traps before capping in the field, the attached seastars eventually must have been swept through the bottom funnel opening for this explanation to be feasible.

The passive sinking hypothesis could not be falsified in most of the field experiments conducted in this study. Thus, hydrodynamical processes must be included in any future studies of processes that determine patterns of larval settlement. However, passive sinking by larvae is not the explicit result of this experimental study. Other processes that could have produced the observed patterns of larval collections among trap designs now must be tested against the passive sinking alternative hypothesis. However, much more information on the

biology and ecology of the larvae collected in this study is required before future process-oriented experiments can be designed.

If larvae sink like passive particles to heights of ~ 50-cm above the seabed, as the results of this study suggest, then it is possible that larvae initially reach the seafloor at sites where particulates, with fall velocities similar to larvae, initially settle. This hypothesis requires experimental testing. Larvae may not remain at these initial settlement sites. Adult distributions of organisms may result from differential mortality of larvae initially deposited over relatively large (tens of meters) areas. Alternatively, once larvae are initially deposited within an area, they may redistribute by actively choosing a microenvironment within that location, by actively swimming above the bottom or remaining on the sediment surface to be resuspended and transported away, by resuspension during storm events, and/or by passive accumulations around microtopographic structures.

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APPENDIX I: Response Time of a Particle to Flow Accelerations

The instantaneous particle velocity, $\vec{u}_p(t)$, can be represented by the following vector equation:

$$\vec{u}_p(t) = \vec{u}_f(t) + \vec{W} + \vec{u}_{ip}(t) \qquad \text{(AI.1)}$$

where $\vec{u}_f(t)$ = the instantaneous fluid velocity, $\vec{W}$ = the particle fall velocity, and $\vec{u}_{ip}(t)$ = the instantaneous inertial velocity of the particle (a deficit velocity of the particle due to fluid accelerations). In a nonaccelerating flow, $\vec{u}_{ip}(t) = 0$ and the path and speed of the particle are determined by $\vec{u}_f(t)$ and $\vec{W}$ alone. As the fluid accelerates from $\vec{u}_f(1)$ to $\vec{u}_f(2)$, the inertial forces on the particle will cause it to lag behind the fluid in reaching $\vec{u}_f(2)$; $\vec{u}_{ip}(t)$ represents this lag, in velocity units. If $\vec{u}_{ip}(t)$ is very small, compared to the other terms in eq. AI.1, then the particle essentially follows the flow.

The governing equations for particle motion in a flow are the particle momentum equations, given here in vector notation:

$$\underset{(A)}{\frac{d\,\vec{u}_p}{dt}} = \underset{(B)}{\frac{1}{S}\frac{d\,\vec{u}_f}{dt}} + \underset{(C)}{\frac{C_m}{S}\frac{d\,(\vec{u}_f-\vec{u}_p)}{dt}} - \underset{(D)}{\frac{3\,C_D(t)}{4\,S\,d}\,(\vec{u}_p-\vec{u}_f)\,(\vec{u}_p-\vec{u}_f)} \underset{(E)}{- \frac{1}{S}(S-1)\,\vec{g}} \qquad \text{(AI.2)}$$

where S = relative density of the particle (ρ_p/ρ_f), C_m = coefficient of mass of the particle, d = particle diameter, $\vec{g}$ = acceleration due to gravity, and $C_D(t)$ = the instantaneous drag

coefficient. As defined by Ho (1964),

$$C_D(t) = \left(\frac{\vec{u}_f - \vec{u}_p}{W}\right)^{-\gamma} C_D \qquad \text{(AI.3)}$$

where C_D = drag coefficient based on the terminal fall speed of the particle (W) and $\gamma = 1$ for the laminar case and $\gamma = 0$ for the turbulent case; $C_D(t)$ is also a function of particle Reynolds number (R_p, defined in Section 2.2) in the accelerating flow, where the characteristic velocity scale is $u_f - u_p$ and the characteristic length scale is d. Term A in eq. AI.2 is the local acceleration of the particle. Terms B and C are the forces conferring forward momentum to the particle, the pressure gradient in the fluid and the inertial force on the particle (the influence of added mass), respectively. Term D is the force resisting the forward motion, the drag force on the particle, and term E is the submerged weight of the particle. Note also that the "Basset" terms are ignored in the force balance.

To solve eq. AI.2 for $\vec{u}_{ip}(t)$, eq. AI.1 is substituted for $\vec{u}_p(t)$ and a perturbation solution (Nielsen 1977) is used to obtain the first order solution. The result is that the response time (T_a) of the particle to a fluid acceleration is approximately

$$\frac{(S+C_m)}{(S-1)} \frac{W}{g} . \qquad \text{(AI.4)}$$

This first order solution for T_a is independent of the fluid acceleration and is primarily controlled by the ratio of particle fall velocity (W) to gravity (g); the ratio of $(S+C_m)$ to (S-1) is

of the order 10^0 for most particles in the ocean (e.g., for quartz grains, $S \simeq 2.65$ and $C_m \simeq 1.5$). Fall velocities of quartz grains range from $< 10^{-3}$ cm/sec (for clays, $d \leq 4 \times 10^{-6}$ μm) to 10^{-1} cm/sec (for silts and very fine sands, $d \leq 10^{-4}$ cm) to 10^{1} cm/sec (for very coarse sands, $d \simeq 10^{-1}$ cm). Because g is of the order 10^3 cm/sec^2, $T_a < 10^{-4}$ sec for all quartz particles less than 10^{-4} cm in diameter; T_a is still only ~ 0.01 sec even for a sand grain 0.10 cm in diameter. In addition, quartz grains are some of the densest naturally occurring particles in the ocean; T_a will be even smaller for lower-density particles.

It appears that the response time of particles to flow accelerations is, for most particles, very small indeed. However, of practical concern is the vertical distance a particle can fall, during T_a, relative to the vertical velocity gradient in the flow. Consider a particle falling through a velocity gradient over a vertical distance z. If the flow accelerates from $\vec{u}_f(1)$ to $\vec{u}_f(2)$ over a distance $z_1 - z_2 = \Delta z$, then the time for the particle to fall this distance is $\Delta z/W$. A particle is considered to be "moving with the flow" (i.e., T_a and, thus, $\vec{u}_{ip}(t)$, are negligible) if the following inequality is satisfied:

$$\frac{(S+C_m)}{(S+1)} \frac{W}{g} \ll \frac{\Delta z}{W} \quad . \tag{AI.5}$$

Clearly, the minimum value for Δz is the particle diameter (d) because velocity changes occurring over a vertical distance less than d would, at most, spin the particle. To conservatively evaluate the

physical limits to this inequality, the upper size limit for very fine sand particles is used as an example, where d is of the order 10^{-4} cm, W is the order 10^{-1} cm/sec and T_a (the left-hand side of eq. AI.5) is of the order 10^{-4} sec. For this example, the smallest value of the right-hand side of eq. AI.5 is 10^{-3} sec. Thus, for less conservative (and more reasonable) values for Δz (i.e., of the order 10^{-3} cm or greater), the inequality will always hold.

This analysis demonstrates that particles essentially follow the flow, when it accelerates, at least for particles $\leq$ 100 μm in diameter and with $\rho_p \leq 2.65$ g/cm^3, or with W $\leq 10^{-1}$ cm/sec. This is the particle range of interest in the present study (see Section 3.4.2). Thus, particles within this range would follow the flow when it accelerates to move over the trap mouth (see Figure 2.9).

APPENDIX II: Additional Results of the Flume Study

In this appendix results of the flume study (Chapter Three) are reported and discussed for cylindrical traps with various aspect ratios and trap Reynolds numbers (R_t) and using several baffling techniques. These results were not presented in Chapter Three for two reasons. (1) These trap designs were selected only to test specific a priori hypotheses that arose from the theoretical analysis of particle trapping, presented in Chapter Two; thus, these trap tests had no direct relevance to the biological hypothesis of interest in this dissertation. (2) Although several of these trap designs had significantly different relative particle collection efficiencies (E_r), they were not selected for use in the field because of considerations of larval biology (see also Section 4.1.1). For example, traps TBC1.7-3.0 and TBC3.6-3.0 have very small mouth diameters relative to the other traps deployed in the field (see Table 3.1); if larvae can perceive and respond to boundaries within a certain radius around them, they may behave differently in the relatively small-diameter versus the larger-diameter traps. Likewise, the honeycomb baffles (described in footnote 12 of Table 3.10) consist of vertical barriers that are very closely packed; the reaction of larvae to such barriers is unknown.

In the first section of this appendix, the a priori hypotheses tested here are stated. In the second section, the results of the trap tests are presented and briefly discussed. All of the methods were described in Chapter Three, Sections 3.2.4 through 3.2.8, but see also the discussion in Sections 3.4.3 and 3.4.4. A summary of these findings is presented in the third section of this appendix.

A.II.1 A priori hypotheses

Several hypotheses regarding the hydrodynamic nature of trap biases were suggested in the theoretical analysis of particle trapping (Chapter Two). Three hypotheses (or predictions) that arose from this theoretical analysis were tested in the present study. Two of the testable predictions concern the importance of resuspension processes to particle trapping. The first hypothesis states that, if resuspension of particles from inside a trap has a significant effect on particle trapping, then in a given flow regime and for traps with the same geometry and mouth diameter (and, thus, the same R_t), particle collection efficiency should increase with increasing trap aspect ratio. Eventually an asymptotic value for particle collection efficiency should be reached; resuspension processes would not be effective for traps with aspect ratios within this asymptotic range.

The second hypothesis concerns the ability of baffles to nullify resuspension effects. Baffles can be viewed as a collection of individual, but adjacent, traps each having a relatively high aspect ratio (the exact ratio depends, of course, on the dimensions of the baffles). Thus, inserting baffles, with relatively high individual cell aspect ratios, into traps with low aspect ratios should increase the particle collection efficiencies of these traps; particle collection efficiencies of such baffled traps are expecteed to fall within the asymptotic range. To test this hypothesis, the baffles must have aspect ratios within the asymptotic range (determined from tests of the first hypothesis) and the trap aspect ratios must be less than the smallest ratio at the asymptote.

The third hypothesis was already stated in Section 2.4.2 and concerns the effect of R_t on particle collection efficiency. This hypothesis states that, for a cylinder, particle collection efficiency should decrease with increasing R_t. However, the range of R_t for which this phenomenon would occur could not be predicted from the theoretical analysis.

To adequately test these hypotheses it is important to hold u_f/W constant, where u_f = the fluid velocity at the height of the trap mouth and W = the particle fall velocity. In addition, R_t must be constant during tests of the resuspension hypotheses and H/D (H = trap height and D = trap mouth diameter) must be held constant during tests of the R_t hypothesis (see results of dimensional analysis, Section 2.2 and discussion of hypotheses in Section 2.4).

A.II.3 Results

In tests of the first hypothesis, collection efficiency significantly increased with increasing aspect ratio, for a range of ratios from 1.0 to 2.7, and the mean E_r values leveled off between the aspect ratios of 2.7 and 3.6. Tests of three cylindrical trap designs (traps OPC8.5-1.0, OPC8.5-1.9 and OPC8.5-2.7) having the same mouth diameter but different aspect ratios (of 1.0, 1.9, and 2.7, respectively) during series 6/7/82 showed an increase in E_r of ~ 40 percent between the aspect ratios of 1.0 and 2.7 (Figure AII.1). The H_o of no difference in collections between the trap designs could be rejected at $\alpha \leq 0.039$ in favor of the ordered H_a that E_r increases with increasing aspect ratio, using the Jonckheere test

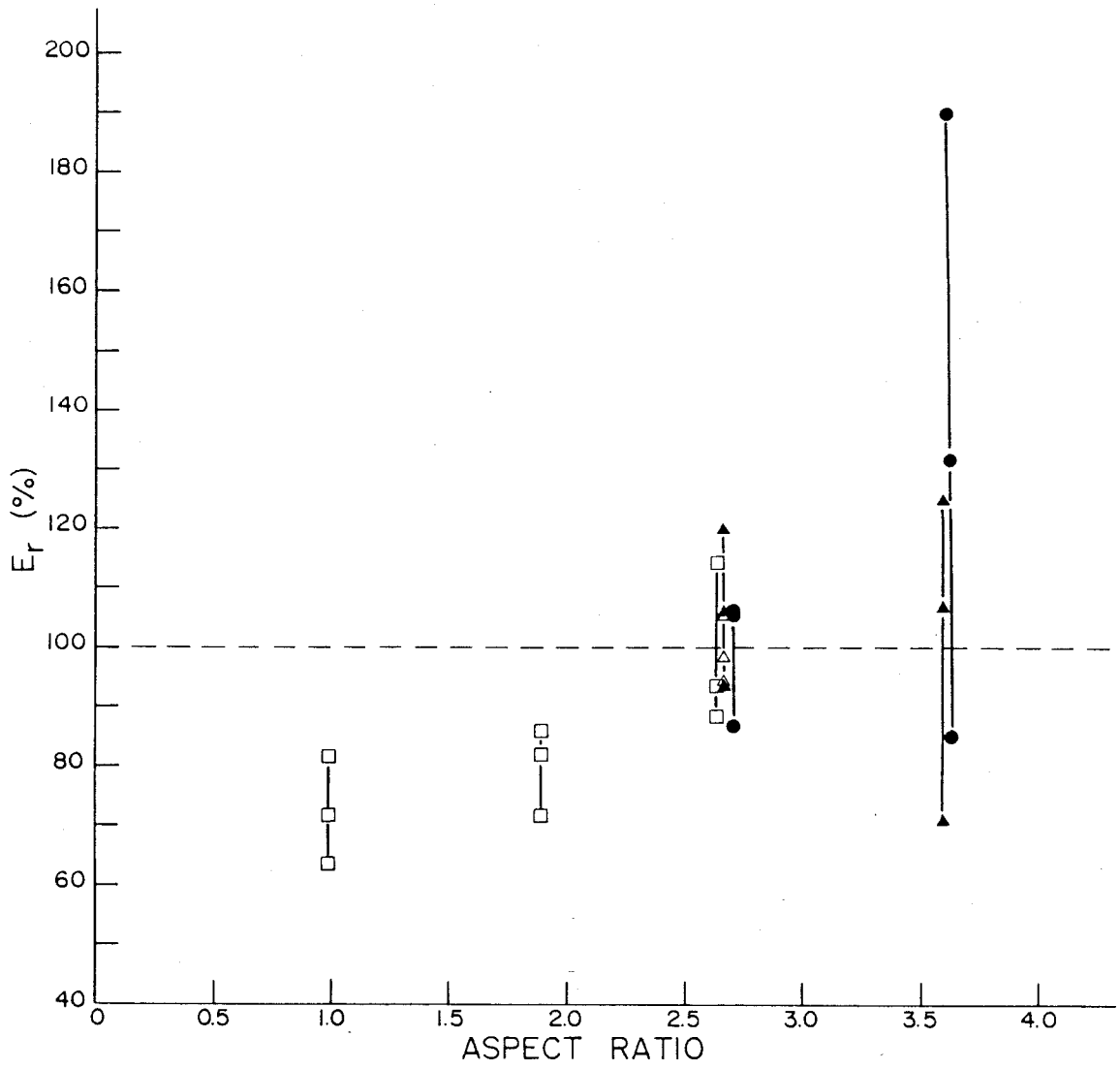

Figure AII.1: Relationship between relative particle collection efficiency and aspect ratio for the cylindrical traps OPC8.5-1.0, OPC8.5-1.9, OPC8.5-2.7 and OPC8.5-3.6. Traps were tested 34-cm above the bottom during series 6/7/82 (open squares) and during 6/24/82 (open triangles). Trap OPC8.5-2.7 was also tested 47-cm above the bottom during series 6/24/82 (solid triangles); trap OPC8.5-3.6 was also tested during this series (solid triangles). During series 8/24/82 all traps were tested 51-cm above the bottom (solid circles). Data only for traps collecting over 8.5-min intervals are shown here. Raw data for calculated E_r values are listed in Appendix III.

(see Section 3.2.8). A higher aspect ratio for the cylindrical trap geometry (trap OPC8.5-3.6, with an aspect ratio of 3.6) was tested during series 6/24/82 and 8/24/82. In both series, collections by this trap design were not significantly different than collections by trap OPC8.5-2.7 (Figure AII.1). In Mann-Whitney U tests, the H_o could be rejected only at $\alpha \leq 0.452$ during series 6/24/82 (using all six replicates of trap OPC8.5-2.7, see Figure AII.1) and the H_o could be rejected only at $\alpha \leq 0.350$ during series 8/24/82, so the H_o was accepted in both cases. However, replicate collections by trap OPC8.5-3.6 were considerably more variable than replicate collections by trap OPC8.5-2.7. For example, the CV of the mean E_r was 38.6 percent for trap OPC8.5-3.6 compared to 10.8 percent for trap OPC8.5-2.7, during series 8/24/82. For this range of aspect ratios, 2.7 appears to be the smallest ratio at the asymptotic mean E_r of ~ 100 percent, but there is evidence that between-replicate variability may increase with increasing aspect ratio.

To test the second hypotheses, honeycomb baffles (described in footnote 12 to Table 3.10) with individual cell aspect ratios of 7.8 were inserted into traps OPC8.5-1.0, OPC8.5-1.9, and OPC8.5-2.7 during series 8/24/82. Care was taken to insure that the top of each baffle was flush with the trap mouth. During this series, two other modifications to trap OPC8.5-2.7 also were tested: screened (see footnote 11 to Table 3.10) traps and traps where the baffle was pushed down to sit on the bottom of the trap; the unmodified trap OPC8.5-2.7 also was tested.

For the top-baffled traps, E_r values again significantly

increased with increasing aspect ratio, this time by ~ 180 percent between the aspect ratios of 1.0 and 2.7 (Figure AII.2). The H_o could be rejected at $\alpha \leq 0.0048$ in favor of the ordered H_a, using the Jonckheere test. These results were not the predicted outcome stated in the second hypothesis.

A comparison of the results for baffled traps tested during series 8/24/82 and unbaffled traps tested during series 6/24/82 (Figure AII.2) indicates that only results for trap OPC8.5-1.0 violated the predictions. E_r values were significantly (i.e., the ranges in E_r values did not overlap) different for baffled versus unbaffled versions of trap OPC8.5-1.9. In fact, baffling this trap design brought the E_r values for trap OPC8.5-1.9 within the range of the E_r values for trap OPC8.5-2.7, as predicted. E_r values overlapped for baffled versus unbaffled versions of trap OPC8.5-2.7, also as predicted, because this trap design has an aspect ratio (of 2.7) at the asymptotic value of E_r (see Figure AII.1). However, E_r values for baffled versions of trap OPC8.5-1.0 were significantly (i.e., the ranges in E_r values did not overlap) lower than for unbaffled traps, by a factor of about two.

Tests of the four versions of trap OPC8.5-2.7 during series 8/24/82 (Figure AII.3) indicate that any obstruction to flow through the trap mouth increases the between-replicate variability in collections, but does not significantly change the mean E_r values. While the ranges in E_r values overlapped for all four trap designs, the percent CV of the mean E_r increased from 10.8 for the unmodified version, to 20.2 for the screened version, to 25.6 for the top-baffled

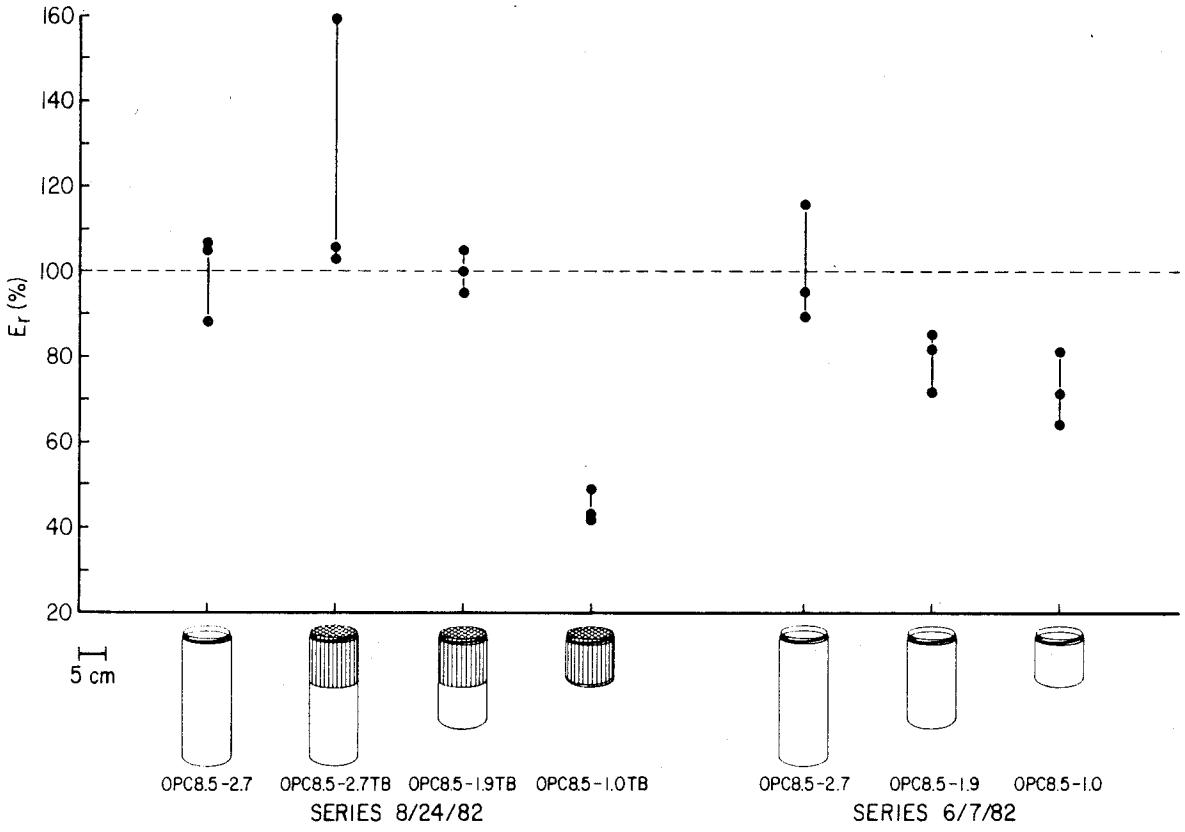

Figure AII.2: Relative particle collection efficiencies for baffled and unbaffled versions of the cylindrical traps OPC8.5-2.7, OPC8.5-1.9 and OPC8.5-1.0. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

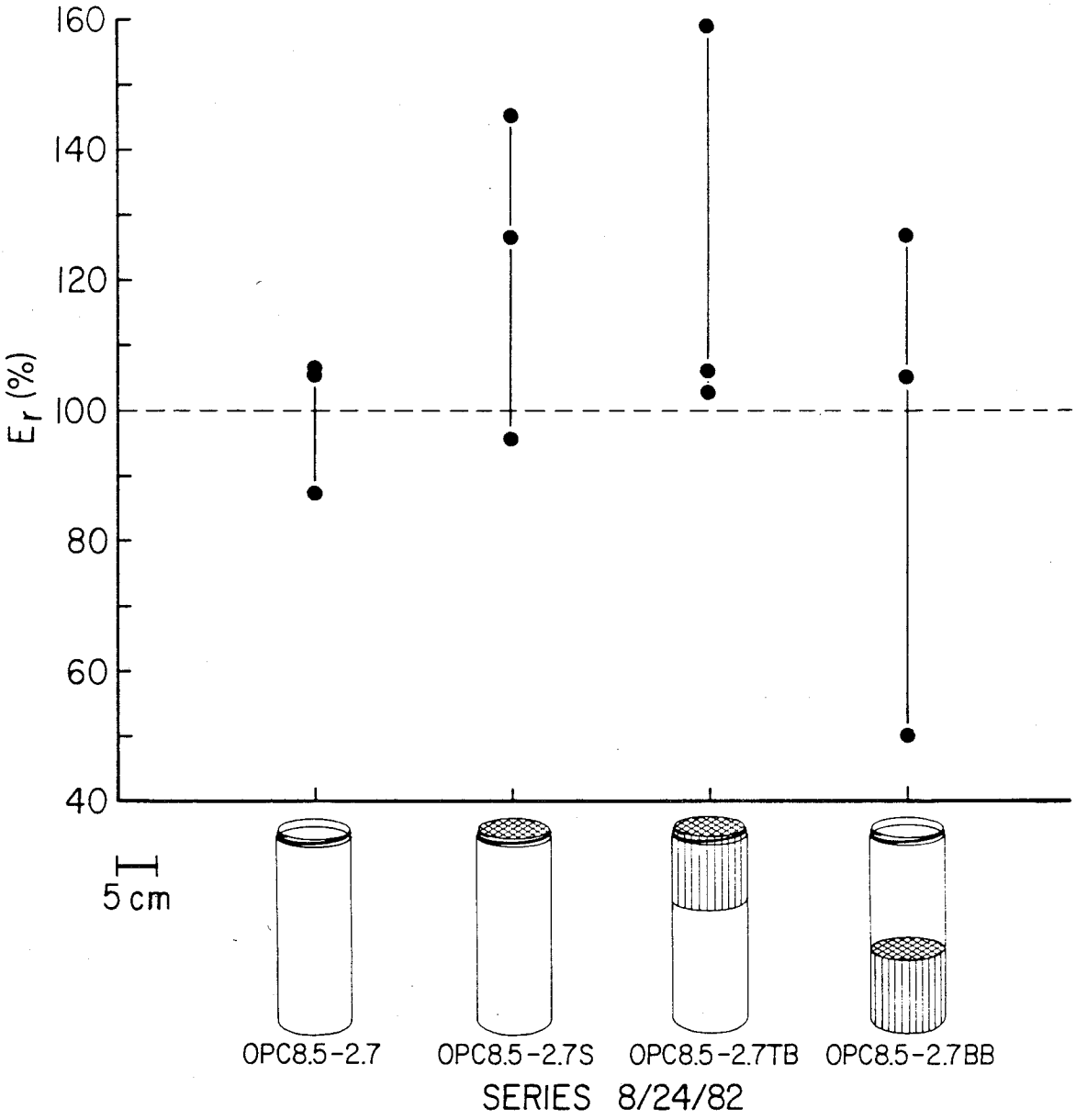

Figure AII.3: Relative particle collection efficiencies for trap OPC8.5-2.7 and for screened and baffled versions of this trap design. Raw data for calculated E_r values are listed in Appendix III. Traps are drawn, to scale, below the Figure.

version, and to 42.0 for the bottom-baffled version.

Predictions of the third hypothesis were confirmed in trap tests during two different series. Three cylindrical trap designs (traps TBC1.7-3.0, TBC3.6-3.1, and TBC7.4-2.9) with similar aspect ratios, but different mouth diameters (and, thus, with R_t values ranging from 2.2×10^3 to 9.2×10^3) tested during series 7/10/82 showed a significant decrease in E_r with increasing R_t (Figure AII.4). The H_0 was rejected at $\alpha \leq 0.0018$ in favor of the ordered H_a, using the Jonckheere test. During series 7/22/82, these three trap designs were tested again, along with even a larger-diameter cylindrical trap design (trap TBC14.7-2.9, with an R_t of 1.8 to 1.9×10^4 during this series). Again, E_r decreased with increasing R_t, but the H_0 could be rejected only at $\alpha \leq 0.0907$, in favor of the ordered H_a (Jonckheere test) for tests during this series. A second test of trap TBC14.7-2.9, during series 8/24/82, yielded E_r values within the range of those determined in series 7/22/82 (Figure AII.4). Thus, for nearly an order of magnitude increase in R_t, the mean E_r dropped by about a factor of two.

A.II.3 Summary

For the three hypotheses presented in Section A.II.1, predictions of the first and the third hypotheses were supported by the experiments conducted in this study. Resuspension was apparently effective in decreasing the particle collection efficiencies of cylindrical traps (8.5 cm in inside mouth diameter) with aspect ratios of 1.0 and 1.9. However, resuspension processes were not

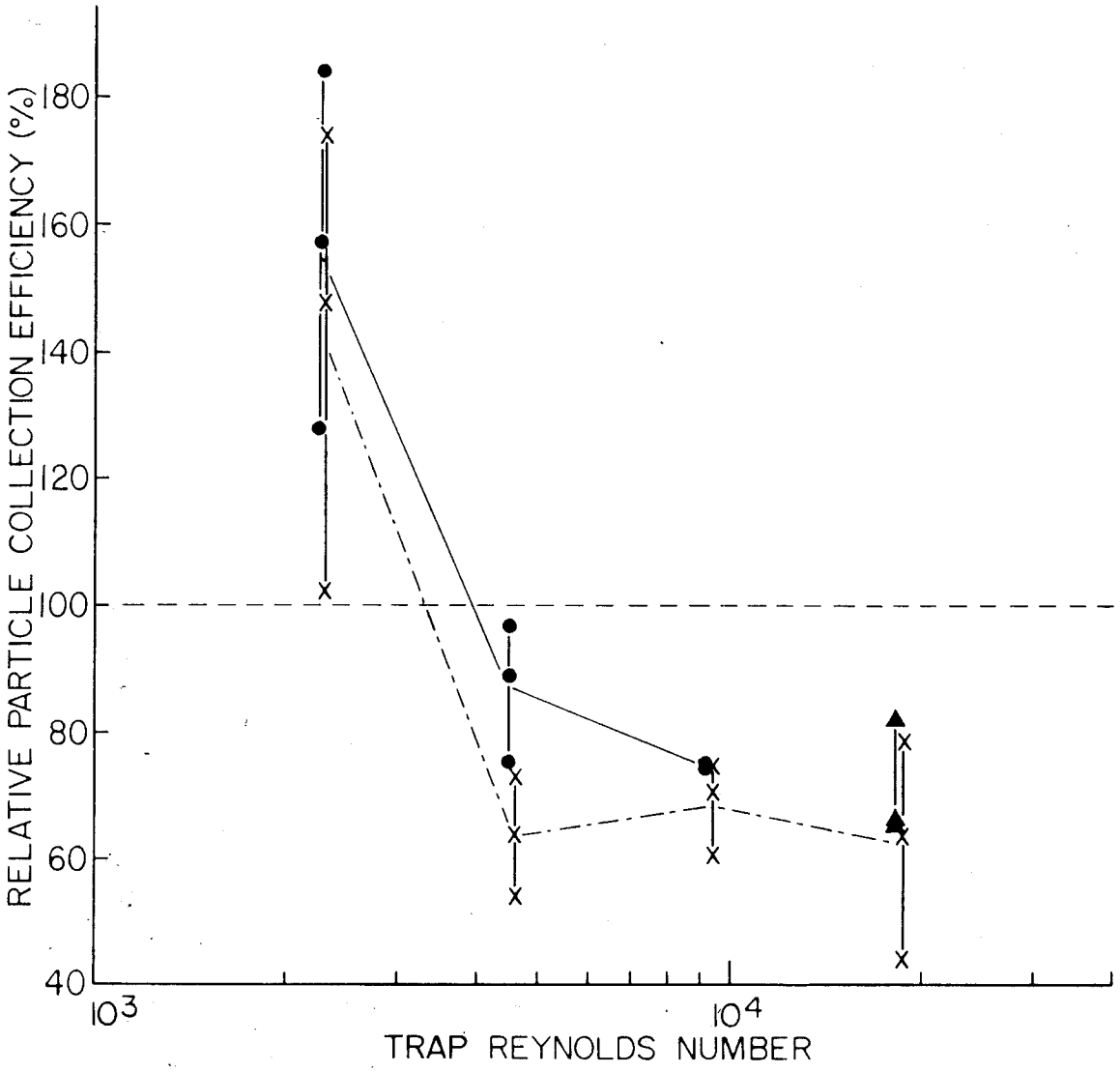

Figure AII.4: Relationship between relative particle collection efficiency and trap Reynolds number for straight-sided cylinders. Traps TBC1.7-3.0, TBC3.6-3.1 and TBC7.4-2.9 were tested during series 7/10/82 (solid circles); these three trap designs and trap TBC14.7-2.9 were tested during series 7/22/82 (crosses) and trap TBC14.7-2.9 was tested again during series 8/24/82 (solid triangles). Raw data are listed in Appendix III.

effective in reducing the mean E_r values for cylindrical traps with the same inside mouth diameter (of 8.5 cm), but aspect ratios of 2.7 and 3.6, indicating that an asymptotic value for particle collection efficiency was reached. However, some physical process, as yet to be determined, was responsible for the increased between-replicate variability for the highest aspect ratio (of 3.6) tested. For traps with aspect ratios of ~ 3.0, particle collection efficiency decreased with increasing R_t, over a range in R_t of approximately one order of magnitude.

For the second hypothesis presented in Section A.II.1, concerning the effectiveness of baffles in counteracting resuspension effects, results of the experiments did not support the predictions for only one of the trap designs tested, the trap with the smallest aspect ratio (of 1.0). In fact, baffling this trap design decreased its particle collection efficiency by nearly a factor of two. This result is puzzling. Baffling traps with higher aspect ratios (of 1.9 and 2.7) had the predicted effect; particle collection efficiencies rose to the asymptotic value for the lower aspect ratio (1.9) and collection efficiencies did not significantly increase for the aspect ratio (2.7) at the asymptotic value. However, screening or baffling either the top or bottom of this trap design (with an aspect ratio of 2.7) considerably increased the between-replicate variability in collections.

It is emphasized that results of the trap tests conducted here apply <u>only</u> to the specific trap designs (cylinders), particle types (spherical glass beads with theoretical fall velocities ranging from

~ 0.014 to ~ 0.22 cm/sec) and flows (unidirectional and turbulent with $u_f \simeq 10$ cm/sec) tested. Additional experimental studies are required to ascertain if the observed phenomena also occur over a wider range of conditions. The results presented here indicate that some trap biases <u>are</u> predictable, at least in a laboratory flume; clearly, more process-oriented studies are required to understand the physics of particle trapping. This study indicates that flux estimates using traps may be difficult to interpret until more experimental work is done to <u>quantify</u> the nature of trap biases.

APPENDIX III: Raw Data for Particle Collection Efficiency Calculations

All relevant data used to calculate trap collection efficiencies and trap Reynolds numbers for each replicate of each trap design are listed in Table A.III.1 in this appendix. Trap designs are listed here by the "codes" assigned in Table 3.1 and data for the three replicates of a given trap design are listed separately. Because flume water height and flume water temperature varied during the course of each series (see Table 3.10), the approximate values (water height to 0.5 cm and water temperature to 0.1°C) are listed separately for the precise intervals during which each replicate was tested. Except for R_t, all terms used here are defined in Section 3.2.7 accompanied by a full description of the calculations necessary to determine these terms. For calculating B_t [= B_f - $(V_t)(C_i-C_{bp})$] and B_p [= $(C_i)(W_c)(A_t)(T_i)$], the value for each series of C_{bp} is listed in Table 3.10. A_t was calculated here using the "Inside Mouth Diameter(s)" listed for the trap designs in Table 3.1, and W_c for each trap collecting interval was taken from Figure 3.10 for the water temperatures listed here. The values of E_s, the mean collection efficiency of trap OPC8.5-2.7, used as a normalizing factor for the collection efficiencies (E) of each replicate (see Section 3.2.7), was calculated separately for each series and is indicated by an asterisk (*). R_t, the trap Reynolds number, is defined in Section 2.2. For the R_t values calculated here, D = "Outside Diameter at Trap Mouth" listed in Table 3.1; u_f = calculated mean flume flow speed at the height of the trap mouth, plotted in Figure 3.18, for the flume water height listed here for each trap collecting interval; and ν = the freshwater kinematic viscosity for the water temperature listed here for each trap collecting interval.

TABLE A.III.1

Raw Data, Calculated Particle Collection Efficiencies, and Calculated Trap Reynolds Numbers for each Replicate of each Trap Design Tested in this Study

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/7/82 (T_i = 510 sec) OPC8.5-2.7										
(1)	59.5	21.5	1.315	5.41 ± 0.51 (10)	46.54	38.11	27.10 ± 2.55	140.6	115.8	1.13
(2)	59.0	21.7	1.360	5.54 ± 0.62 (10)	39.21	30.31	27.88 ± 3.12	108.7	89.5	1.15
(3)	59.0	21.7	1.330	4.88 ± 0.25 (9)	39.73	31.91	27.77 ± 1.27	114.9	94.6	1.16
							mean =	121.4*	100.0	
							SD =	16.9	13.9	
							CV =	13.9	13.9	
OPC8.5-1.9										
(1)	59.5	21.5	0.950	6.09 ± 0.32 (8)	38.44	31.70	30.50 ± 1.60	103.9	85.6	1.13
(2)	59.5	21.7	0.950	6.16 ± 0.90 (8)	37.70	30.90	31.00 ± 4.53	99.7	82.1	1.14
(3)	58.5	22.2	0.960	4.78 ± 0.41 (10)	26.86	21.31	24.32 ± 2.09	87.6	72.2	1.17
							mean =	97.1	80.0	
							SD =	8.5	7.0	
							CV =	8.7	8.7	

TABLE A.III.1 (cont. - 2)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 6/7/82 (T_i = 510 sec) (cont.)										
OPC8.5-1.0										
(1)	59.0	22.0	0.485	4.97 ± 1.09 (9)	27.89	24.99	25.17 ± 5.52	99.3	81.8	1.15
(2)	59.0	22.1	0.490	5.39 ± 0.36 (10)	27.21	24.08	27.36 ± 1.83	88.0	72.5	1.16
(3)	59.0	22.2	0.465	5.14 ± 0.49 (10)	23.33	20.47	26.15 ± 2.49	78.3	64.5	1.16
							mean =	88.5	72.9	
							SD =	10.5	8.7	
							CV =	11.9	11.9	
OPF8.5-1.9 (without funnel-washings)										
(1)	59.5	21.6	0.465	6.23 ± 0.25 (9)	14.48	11.12	31.30 ± 1.26	35.5	29.2	1.12
(2)	59.0	21.9	0.480	4.92 ± 0.53 (10)	9.34	6.50	24.87 ± 2.68	23.8	19.6	1.15
(3)	59.0	21.9	0.455	5.55 ± 0.72 (10)	8.73	5.75	28.06 ± 3.83	20.5	16.9	1.15
							mean =	26.6	21.9	
							SD =	7.9	6.5	
							CV =	29.7	29.7	

TABLE A.III.1 (cont. - 3)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 6/7/82 (T_i = 390 sec) OPC8.5-2.7										
(1)	60.0	21.0	1.370	6.73 ± 0.99 (8)	36.81	26.22	25.47 ± 3.75	102.9	84.8	1.11
(2)	59.5	21.2	1.340	6.82 ± 0.36 (7)	41.10	30.62	25.94 ± 1.37	118.0	97.2	1.12
(3)	59.5	21.2	0.975	6.39 ± 0.49 (8)	33.84	26.63	24.31 ± 1.86	109.5	90.2	1.12
							mean =	110.1	90.7	
							SD =	7.6	6.2	
							CV =	6.8	6.8	
OPC8.5-1.9										
(1)	60.5	20.6	0.945	6.93 ± 0.60 (8)	31.05	23.56	25.99 ± 2.25	90.6	74.6	1.09
(2)	60.0	20.7	0.895	6.45 ± 0.82 (8)	36.17	29.50	24.25 ± 3.08	121.6	100.2	1.10
							mean =	106.1	87.4	
							SD =	21.9	18.1	
							CV =	20.7	20.7	

TABLE A.III.1 (cont. - 4)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/7/82 (T_i = 390 sec) (cont.)										
OPC8.5-1.0										
(1)	60.0	20.7	0.475	6.85 ± 0.46 (7)	30.46	26.73	25.75 ± 1.73	103.8	85.5	1.10
(2)	60.0	20.8	0.480	6.69 ± 0.82 (8)	29.58	25.89	25.21 ± 3.09	102.7	84.6	1.10
(3)	60.0	20.9	0.490	7.41 ± 0.64 (8)	29.16	25.04	27.99 ± 2.42	89.5	73.7	1.10
							mean =	98.7	81.3	
							SD =	8.0	6.6	
							CV =	8.1	8.1	
OPF8.5-1.9 (without funnel-washings)										
(1)	60.0	20.9	0.460	7.77 ± 0.32 (8)	19.19	15.16	29.35 ± 1.21	51.6	42.5	1.10
(2)	60.0	21.1	0.470	6.23 ± 0.60 (8)	12.27	8.87	23.64 ± 2.28	37.5	30.9	1.11
(3)	60.0	21.1	0.405	7.02 ± 0.64 (7)	15.93	12.68	26.64 ± 2.43	47.6	39.2	1.11
							mean =	45.6	37.5	
							SD =	7.3	6.0	
							CV =	16.0	16.0	

TABLE A.III.1 (cont. - 5)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/7/82 (T_i = 270 sec) OPC8.5-2.7										
(1)	61.0	19.9	1.345	8.27 ± 0.63 (6)	36.75	24.28	21.13 ± 1.61	114.9	94.6	1.06
(2)	60.5	20.1	1.350	7.69 ± 0.63 (6)	30.57	18.83	19.73 ± 1.62	95.4	78.6	1.08
(3)	60.5	20.3	1.320	7.83 ± 0.57 (5)	31.97	20.31	20.18 ± 1.47	100.6	82.9	1.08
							mean =	103.6	85.4	
							SD =	10.1	8.3	
							CV =	9.7	9.7	
OPC8.5-1.9										
(1)	60.5	20.1	0.940	8.24 ± 0.48 (6)	29.03	20.34	21.14 ± 1.23	96.2	79.2	1.08
(2)	60.5	20.4	0.930	8.28 ± 0.75 (6)	26.45	17.82	21.40 ± 1.94	83.3	68.6	1.08
(3)	60.5	20.5	0.940	7.58 ± 0.56 (5)	26.64	18.57	19.62 ± 1.45	94.6	77.9	1.09
							mean =	91.4	75.2	
							SD =	7.0	5.8	
							CV =	7.7	7.7	

TABLE A.III.1 (cont. - 6)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/7/82 (T_i = 270 sec) (cont.)										
OPC8.5-1.0										
(1)	60.5	20.2	0.490	7.96 ± 0.45 (6)	15.97	11.58	20.47 ± 1.16	56.6	46.6	1.08
(2)	60.5	20.4	0.480	8.03 ± 0.17 (6)	24.36	20.03	20.75 ± 0.44	96.5	79.5	1.08
(3)	60.5	20.5	0.480	8.06 ± 0.32 (6)	22.44	18.09	20.87 ± 0.83	86.7	71.4	1.09
							mean =	79.9	65.8	
							SD =	20.8	17.1	
							CV =	26.0	26.0	
OPF8.5-1.9 (without funnel-washings)										
(1)	61.0	20.0	0.450	8.04 ± 0.34 (6)	12.42	8.35	20.57 ± 0.87	40.6	33.4	1.07
(2)	60.5	20.2	0.470	7.81 ± 0.56 (6)	8.38	4.24	20.09 ± 1.44	21.1	17.4	1.08
(3)	60.5	20.3	0.475	7.60 ± 0.40 (6)	8.74	4.66	19.58 ± 1.03	23.8	19.6	1.08
							mean =	28.5	23.5	
							SD =	10.6	8.7	
							CV =	37.0	37.0	

TABLE A.III.1 (cont. - 7)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 6/24/82 (T_i = 510 sec)										
OPC8.5-2.7 (47-cm above bottom; all other trap mouths were 34-cm above bottom)										
(1)	69.5	22.6	1.340	10.82 ± 0.65 (10)	29.05	13.87	15.94 ± 0.96	87.0	105.8	0.98
(2)	69.0	23.4	1.370	14.61 ± 0.64 (10)	38.50	17.79	21.90 ± 0.96	81.2	98.8	1.02
(3)	68.5	23.8	1.365	15.18 ± 0.61 (10)	39.45	18.03	22.97 ± 0.92	78.5	95.5	1.03
							mean =	82.2*	100.0	
							SD =	4.3	5.3	
							CV =	5.3	5.3	
OPC8.5-2.7										
(1)	69.5	22.3	1.355	11.39 ± 0.79 (10)	29.56	13.44	16.64 ± 1.15	80.8	98.3	0.89
(2)	69.5	22.4	1.335	10.36 ± 0.44 (10)	29.55	15.04	15.17 ± 0.64	99.1	120.6	0.89
(3)	69.5	22.6	1.340	11.20 ± 0.44 (10)	30.10	11.71	16.50 ± 0.65	87.3	106.2	0.90
							mean =	89.1	108.4	
							SD =	9.3	11.3	
							CV =	10.4	10.4	

TABLE A.III.1 (cont. - 8)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 6/24/82 (T_i = 510 sec) (cont.) OPC8.5-3.6										
(1)	69.0	23.3	1.805	13.45 ± 0.59 (10)	44.13	18.93	20.12 ± 0.88	94.1	114.5	1.02
(2)	68.5	23.5	1.840	14.06 ± 0.78 (10)	45.30	18.49	21.16 ± 1.17	87.4	106.3	1.02
(3)	67.5	24.6	1.825	11.25 ± 0.93 (10)	32.11	10.65	17.35 ± 1.43	61.4	74.7	1.07
							mean =	81.0	98.5	
							SD =	17.3	21.0	
							CV =	21.3	21.3	
SERIES 6/24/82 (T_i = 390 sec) OPC8.5-2.7										
(1)	70.0	22.1	1.315	9.35 ± 0.86 (8)	27.06	14.09	10.39 ± 0.96	135.6	165.0	0.98
(2)	69.0	23.2	1.360	12.86 ± 0.48 (8)	32.39	14.21	14.68 ± 0.55	96.8	117.8	1.02
(3)	69.0	23.5	1.365	13.61 ± 0.47 (8)	34.14	14.87	15.66 ± 0.54	95.0	115.6	1.02
							mean =	109.1	132.8	
							SD =	22.9	27.9	
							CV =	21.0	21.0	

TABLE A.III.1 (cont. - 9)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/24/82 (T_i = 390 sec) (cont.) OPC8.5-3.6										
(1)	69.5	22.5	1.825	10.79 ± 0.29 (8)	33.08	12.46	12.11 ± 0.32	102.9	125.2	0.98
(2)	68.0	24.2	1.830	14.80 ± 0.42 (8)	43.25	15.23	17.29 ± 0.49	88.1	107.2	1.05
(3)	67.5	24.6	1.835	10.17 ± 0.46 (8)	26.65	10.68	12.00 ± 0.54	58.8	71.5	1.07
							mean =	83.3	101.3	
							SD =	22.4	27.3	
							CV =	26.9	26.9	
SERIES 6/24/82 (T_i = 270 sec) OPC8.5-2.7										
(1)	69.5	22.7	1.355	10.48 ± 0.54 (6)	23.10	8.21	8.19 ± 0.42	100.2	121.9	0.98
(2)	69.0	23.3	1.340	13.19 ± 0.74 (6)	29.68	11.32	10.45 ± 0.59	108.3	131.8	1.02
(3)	68.0	24.4	1.347	13.71 ± 0.57 (6)	25.46	6.31	11.13 ± 0.46	56.7	69.0	1.06
							mean =	88.4	107.6	
							SD =	27.8	33.8	
							CV =	31.4	31.4	

TABLE A.III.1 (cont. - 10)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 6/24/82 (T_i = 270 sec) (cont.) OPC8.5-3.6										
(1)	69.5	22.3	1.830	9.52 ± 0.75 (6)	27.50	9.14	7.37 ± 0.58	124.0	150.8	0.99
(2)	69.0	23.2	1.800	14.22 ± 0.24 (6)	35.31	8.80	11.24 ± 0.19	78.3	95.3	1.02
(3)	68.0	24.0	1.835	14.62 ± 0.34 (6)	38.53	10.77	11.76 ± 0.27	91.6	111.4	1.05
							mean =	98.0	119.2	
							SD =	23.5	28.6	
							CV =	24.0	24.0	
SERIES 6/24/82 (T_i = 990 sec) OPC8.5-2.7										
(1)	69.5	22.8	1.315	10.21 ± 0.96 (18)	43.55	29.45	29.31 ± 2.76	100.5	122.3	0.99
(2)	68.0	24.3	1.355	14.96 ± 0.78 (18)	55.04	34.08	44.45 ± 2.32	76.7	93.3	1.06
(3)	67.5	24.7	1.360	8.54 ± 1.31 (18)	26.08	13.77	25.62 ± 3.93	53.7	65.3	1.07
							mean =	77.0	93.6	
							SD =	23.4	28.5	
							CV =	30.4	30.4	

TABLE A.III.1 (cont. - 11)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 6/24/82 (T_i = 990 sec) (cont.) OPC8.5-3.6										
(1)	68.5	23.7	1.835	14.26 ± 0.75 (18)	61.86	34.76	41.81 ± 2.20	83.1	101.1	1.03
(2)	68.0	24.1	1.800	15.19 ± 0.40 (17)	62.89	34.63	44.97 ± 1.18	77.0	93.7	1.05
(3)	67.5	24.5	1.815	12.66 ± 0.80 (18)	49.45	25.54	37.83 ± 2.39	67.5	82.1	1.06
							mean =	75.9	92.3	
							SD =	7.9	9.6	
							CV =	10.4	10.4	
SERIES 7/10/82 (T_i = 510 sec) OPC8.5-2.7										
(1)	68.5	24.0	1.407	9.07 ± 0.29 (6)	26.78	12.06	13.78 ± 0.44	87.5	106.8	1.04
(2)	71.0	24.5	1.370	9.73 ± 0.33 (6)	29.74	14.51	14.98 ± 0.51	96.9	118.3	1.01
(3)	70.0	25.0	1.353	12.14 ± 0.10 (6)	29.90	11.59	12.14 ± 0.10 (6)	61.2	74.7	1.04
							mean =	81.9*	99.9	
							SD =	18.5	22.6	
							CV =	22.6	22.6	

TABLE A.III.1 (cont. - 12)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 7/10/82 (T_i = 510 sec) (cont.)										
OPC8.5-2.7S										
(1)	71.5	24.2	1.360	8.50 ± 0.28 (6)	29.84	16.39	12.99 ± 0.43	126.2	154.1	1.00
(2)	70.5	24.6	1.360	10.43 ± 0.46 (6)	29.94	13.86	16.09 ± 0.71	86.1	105.1	1.02
(3)	70.5	24.7	1.370	10.71 ± 0.44 (6)	30.03	13.45	16.55 ± 0.68	81.3	99.3	1.03
							mean =	97.9	119.3	
							SD =	24.6	30.1	
							CV =	25.2	25.2	
OPG8.3-3.0										
(1)	71.5	24.1	3.770	8.85 ± 0.49 (5)	62.71	24.11	12.87 ± 0.71	187.3	228.7	0.98
(2)	69.0	25.7	3.780	11.66 ± 0.40 (6)	76.87	27.54	17.60 ± 0.60	156.5	191.1	1.05
(3)	69.0	25.8	3.825	11.40 ± 0.41 (6)	77.19	28.27	17.24 ± 0.62	164.0	200.2	1.06
							mean =	169.3	206.7	
							SD =	16.1	19.6	
							CV =	9.5	5.2	

TABLE A.III.1 (cont. - 13)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 7/10/82 (T_i = 510 sec) (cont.)										
TBC7.4-2.9										
(1)	70.0	25.0	0.840	12.03 ± 0.78 (6)	19.94	8.67	14.20 ± 2.10	61.1	74.6	0.90
(2)	70.0	25.4	0.910	11.41 ± 0.24 (6)	19.98	8.33	13.59 ± 0.29	61.3	74.8	0.92
							mean =	61.2	74.7	
							SD =	0.1	0.1	
							CV =	0.1	0.1	
TBC3.6-3.1										
(1)	68.5	23.9	0.114	9.02 ± 0.28 (6)	3.14	1.95	2.45 ± 0.08	79.6	97.2	0.45
(2)	70.5	24.9	0.114	11.87 ± 0.26 (6)	3.56	2.05	3.31 ± 0.07	61.9	75.6	0.45
(3)	70.0	25.4	0.116	11.46 ± 0.24 (6)	3.84	2.35	3.23 ± 0.07	72.8	88.9	0.46
							mean =	71.4	87.2	
							SD =	8.9	10.9	
							CV =	12.5	12.5	

TABLE A.III.1 (cont. - 14)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 7/10/82 (T_i = 510 sec) (cont.)										
TBC1.7-3.0										
(1)	70.5	24.7	0.012	10.89 ± 0.35 (6)	1.01	0.86	0.67 ± 0.02	128.4	156.8	0.22
(2)	70.0	25.2	0.012	10.41 ± 0.47 (6)	0.82	0.68	0.65 ± 0.03	104.6	127.7	0.23
(3)	70.0	25.2	0.012	10.79 ± 0.25 (4)	1.15	1.00	0.67 ± 0.02	149.2	182.2	0.23
							mean =	127.4	155.6	
							SD =	22.3	27.3	
							CV =	17.5	17.5	
OPF8.3-1.9 (without funnel-washings)										
(1)	69.5	25.5	0.345	11.38 ± 0.27 (6)	11.90	7.49	17.08 ± 0.40	43.8	53.5	1.06
(2)	69.5	25.6	0.465	12.12 ± 0.81 (6)	12.78	6.50	18.26 ± 1.22	35.6	43.5	1.07
(3)	69.5	25.7	0.355	11.53 ± 0.30 (6)	8.71	4.12	17.40 ± 0.45	23.7	28.9	1.07
							mean =	34.4	42.0	
							SD =	10.1	12.4	
							CV =	29.5	29.5	

TABLE A.III.1 (cont. - 15)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 7/10/82 (T_i = 510 sec) (cont.) OPF8.3-1.9 (with funnel-washings)										
(1)	69.5	25.5	0.345	11.38 ± 0.27 (6)	17.43	13.02	17.08 ± 0.40	76.2	93.0	1.06
(2)	69.5	25.6	0.465	12.12 ± 0.81 (6)	17.77	11.49	18.26 ± 1.22	62.9	76.8	1.07
(3)	69.5	25.7	0.355	11.53 ± 0.30 (6)	15.26	10.67	17.40 ± 0.45	61.3	74.9	1.07
							mean =	66.8	81.6	
							SD =	8.2	9.9	
							CV =	12.1	12.1	
SERIES 7/22/82 (T_i = 510 sec) OPC8.5-2.7										
(1)	71.5	26.8	1.350	10.32 ± 0.33 (6)	31.38	15.67	16.72 ± 0.53	93.7	76.0	1.07
(2)	70.0	27.4	1.350	7.79 ± 0.38 (6)	30.08	17.78	12.78 ± 0.62	139.1	112.8	1.10
(3)	69.5	27.7	1.320	9.06 ± 0.49 (6)	34.22	20.52	14.97 ± 0.81	137.1	111.2	1.12
							mean =	123.3*	100.0	
							SD =	25.6	20.8	
							CV =	20.8	20.8	

TABLE A.III.1 (cont. - 16)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 7/22/82 (T_i = 510 sec) (cont.)										
OPG8.3-3.0										
(1)	73.5	25.8	3.700	8.22 ± 1.11 (5)	70.26	34.96	12.46 ± 1.68	281.3	228.1	0.99
(2)	71.0	27.0	3.775	9.70 ± 0.29 (6)	71.12	29.52	15.07 ± 0.45	195.9	158.9	1.04
(3)	70.5	27.2	3.785	9.20 ± 0.69 (6)	69.84	30.02	14.34 ± 1.08	209.3	169.7	1.06
							mean =	228.8	185.6	
							SD =	45.9	37.2	
							CV =	20.0	20.0	
TBC14.7-2.9										
(1)	73.0	26.0	7.240	10.48 ± 0.51 (6)	112.67	27.24	49.89 ± 2.43	54.6	44.3	1.83
(2)	72.5	26.5	7.185	8.98 ± 0.26 (6)	115.91	41.90	43.22 ± 1.25	96.9	78.6	1.85
(3)	71.5	26.7	7.050	9.72 ± 0.17 (6)	114.75	36.92	47.03 ± 0.82	78.5	63.7	1.90
							mean =	76.7	62.2	
							SD =	21.2	17.2	
							CV =	27.6	27.6	

TABLE A.III.1 (cont. - 17)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 7/22/82 (T_i = 510 sec) (cont.)										
TBC7.4-2.9										
(1)	73.0	26.2	0.915	10.65 ± 0.21 (6)	20.53	9.58	12.92 ± 0.25	74.1	60.1	0.91
(2)	72.0	26.5	0.900	9.13 ± 0.48 (6)	19.07	9.66	11.13 ± 0.58	86.8	70.4	0.93
(3)	71.5	26.9	0.915	10.09 ± 0.22 (6)	20.25	9.81	12.42 ± 0.27	91.9	74.5	0.95
							mean =	84.3	68.3	
							SD =	9.2	7.4	
							CV =	10.8	10.8	
TBC3.6-3.1										
(1)	73.5	25.9	0.116	10.21 ± 0.36 (6)	3.27	1.93	2.91 ± 0.10	66.3	53.8	0.44
(2)	73.0	26.2	0.116	9.35 ± 0.49 (6)	3.64	2.40	2.68 ± 0.14	89.6	72.7	0.45
(3)	70.5	27.2	0.117	10.15 ± 0.31 (6)	3.68	2.34	2.98 ± 0.09	78.5	63.7	0.47
							mean =	78.1	63.4	
							SD =	11.6	9.4	
							CV =	14.8	14.8	

TABLE A.III.1 (cont. - 18)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 7/22/82 (T_i = 510 sec) (cont.)										
TBC1.7-3.0										
(1)	73.0	26.1	0.013	8.78 ± 0.83 (6)	1.15	1.02	0.56 ± 0.05	182.1	147.7	0.22
(2)	71.5	26.8	0.014	10.28 ± 0.45 (6)	1.00	0.84	0.67 ± 0.03	125.4	101.7	0.23
(3)	70.5	27.2	0.013	9.52 ± 0.86 (6)	1.47	1.33	0.62 ± 0.06	214.5	174.0	0.24
							mean =	174.0	141.1	
							SD =	45.1	36.6	
							CV =	25.9	25.9	
OPF14.1-1.6 (with funnel-washings)										
(1)	72.5	26.3	1.650	10.62 ± 0.16 (6)	54.19	34.49	46.85 ± 0.71	73.6	59.7	1.72
(2)	70.0	27.3	1.865	8.07 ± 0.36 (6)	55.59	38.08	36.37 ± 1.62	104.7	84.9	1.83
(3)	69.5	27.7	1.850	8.23 ± 0.46 (6)	55.66	37.99	37.42 ± 2.09	101.5	82.3	1.87
							mean =	93.3	75.6	
							SD =	17.1	13.9	
							CV =	18.4	18.4	

TABLE A.III.1 (cont. - 19)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) OPC8.5-2.7										
(1)	73.5	25.3	1.360	9.33 ± 0.93 (6)	51.51	36.86	14.63 ± 1.46	251.9	107.0	1.00
(2)	72.5	26.2	1.365	9.74 ± 0.76 (6)	53.99	38.73	15.59 ± 1.18	248.4	105.5	1.03
(3)	74.0	26.7	1.350	10.51 ± 0.87 (6)	51.16	35.03	17.00 ± 1.41	206.1	87.5	1.02
							mean =	235.5*	100.0	
							SD =	25.5	10.8	
							CV =	10.8	10.8	
OPC8.5-2.7S										
(1)	74.5	25.1	1.335	9.21 ± 0.95 (6)	63.31	49.09	14.36 ± 1.48	341.8	145.1	0.99
(2)	70.5	26.5	1.320	10.37 ± 0.33 (6)	53.29	37.70	16.68 ± 0.53	226.0	96.0	1.07
(3)	69.5	26.6	1.350	10.22 ± 0.52 (6)	64.89	49.15	16.50 ± 0.84	297.9	126.5	1.09
							mean =	288.6	122.5	
							SD =	58.5	24.8	
							CV =	20.2	20.2	

TABLE A.III.1 (cont. - 20)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) (cont.)										
OPP8.3-2.7										
(1)	74.0	26.1	1.465	10.55 ± 0.27 (6)	36.46	18.89	16.07 ± 0.41	117.5	49.9	1.76
(2)	72.0	27.0	1.450	10.57 ± 0.51 (6)	33.31	15.90	16.42 ± 0.79	96.8	41.1	1.85
(3)	69.5	27.2	1.455	10.34 ± 0.44 (6)	32.62	15.48	16.12 ± 0.69	96.0	40.8	1.93
							mean =	103.4	43.9	
							SD =	12.2	5.2	
							CV =	11.8	11.8	
OPC8.5-2.7BB										
(1)	73.0	25.4	1.345	10.63 ± 0.10 (6)	66.04	49.81	16.70 ± 0.16	298.3	126.7	1.01
(2)	71.5	27.0	1.360	10.43 ± 1.31 (6)	58.14	42.00	16.99 ± 2.13	247.2	105.0	1.07
(3)	69.0	27.3	1.335	8.90 ± 0.21 (6)	31.04	17.24	14.58 ± 0.34	118.2	50.2	1.12
							mean =	221.2	94.0	
							SD =	92.8	39.4	
							CV =	42.0	42.0	

TABLE A.III.1 (cont. - 21)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_f = 510 sec) (cont.)										
OPC8.5-2.7TB										
(1)	74.5	26.0	1.355	10.28 ± 0.31 (6)	77.16	61.28	16.36 ± 0.49	374.6	159.1	1.01
(2)	71.5	27.0	1.350	11.01 ± 0.68 (5)	60.34	43.53	17.97 ± 1.11	242.6	103.0	1.07
(3)	70.0	27.1	1.340	9.90 ± 0.47 (6)	55.66	40.46	16.16 ± 0.76	250.4	106.3	1.09
							mean =	289.2	122.8	
							SD =	74.1	31.5	
							CV =	25.6	25.6	
OPC8.5-1.9TB										
(1)	71.5	25.5	0.930	9.58 ± 0.32 (4)	45.92	35.67	15.08 ± 0.50	236.5	100.4	1.13
(2)	71.5	26.4	0.940	10.24 ± 0.37 (6)	51.76	40.78	16.45 ± 0.59	247.9	105.3	1.14
(3)	70.0	26.6	0.950	10.50 ± 0.96 (6)	49.26	37.92	16.95 ± 1.55	223.7	95.0	1.17
							mean =	236.0	100.2	
							SD =	12.1	5.2	
							CV =	5.2	5.2	

TABLE A.III.1 (cont. - 22)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) (cont.)										
OPC8.5-1.0TB										
(1)	71.0	25.8	0.460	9.89 ± 0.65 (6)	21.20	15.99	15.68 ± 1.03	102.0	43.3	1.04
(2)	73.0	26.2	0.465	10.11 ± 0.33 (6)	21.44	16.07	16.18 ± 0.53	99.3	42.2	1.03
(3)	72.5	26.9	0.470	9.22 ± 0.30 (6)	21.89	16.88	14.97 ± 0.49	112.8	47.9	1.05
							mean =	104.7	44.5	
							SD =	7.1	3.0	
							CV =	6.7	6.7	
OPC8.5-3.6										
(1)	72.0	26.1	1.810	9.18 ± 1.04 (6)	84.78	65.56	14.66 ± 1.66	447.2	189.9	1.04
(2)	70.5	26.5	1.815	10.38 ± 0.32 (6)	73.52	52.07	16.70 ± 0.51	311.8	132.4	1.07
(3)	73.5	26.9	1.805	10.40 ± 0.72 (6)	55.26	33.89	16.88 ± 1.17	200.8	85.3	1.04
							mean =	319.9	135.9	
							SD =	123.4	52.4	
							CV =	38.6	38.6	

TABLE A.III.1 (cont. - 23)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) (cont.)										
OPGC8.5-3.6										
(1)	71.5	25.6	4.170	10.20 ± 0.36 (6)	136.07	87.53	16.09 ± 0.57	544.0	231.0	1.04
(2)	71.0	25.9	4.150	9.92 ± 0.28 (6)	143.10	95.96	15.76 ± 0.45	608.9	258.6	1.04
(3)	71.5	26.4	4.130	9.75 ± 0.24 (6)	123.77	77.56	15.66 ± 0.38	495.3	210.3	1.06
							mean =	549.4	233.3	
							SD =	57.0	24.2	
							CV =	10.4	10.4	
OPG8.3-3.0										
(1)	71.5	25.7	3.785	10.56 ± 0.17 (6)	139.57	94.15	15.91 ± 0.26	591.8	251.3	1.02
(2)	71.5	25.7	3.780	10.82 ± 0.31 (6)	130.82	84.48	16.30 ± 0.47	518.3	220.1	1.02
(3)	73.0	26.9	3.800	9.21 ± 0.27 (6)	112.29	71.82	14.26 ± 0.42	503.6	213.8	1.02
							mean =	537.9	228.4	
							SD =	47.2	20.1	
							CV =	8.8	8.8	

TABLE A.III.1 (cont. - 24)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) (cont.) OPG8.3-3.0S										
(1)	72.5	25.4	3.830	10.34 ± 0.41 (6)	130.75	85.63	15.49 ± 0.61	552.8	234.7	0.99
(2)	71.5	25.8	3.805	10.42 ± 0.21 (6)	136.21	91.08	15.76 ± 0.32	577.9	245.4	1.02
							mean =	565.4	240.0	
							SD =	17.7	7.6	
							CV =	3.2	3.2	
TBC14.7-2.9										
(1)	74.5	25.1	7.150	8.83 ± 0.53 (6)	153.18	79.75	41.20 ± 2.47	193.6	82.2	1.76
(2)	71.0	26.5	7.265	10.98 ± 1.01 (6)	170.96	80.73	52.84 ± 4.86	152.8	64.9	1.88
(3)	74.0	26.8	7.185	10.90 ± 1.07 (6)	170.03	81.37	52.83 ± 5.19	154.0	65.4	1.83
							mean =	166.8	70.8	
							SD =	23.2	9.8	
							CV =	13.8	13.8	

TABLE A.III.1 (cont. - 25)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ()=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t (x10^4)
SERIES 8/24/82 (T_i = 510 sec) (cont.)										
TBC14.7-1.6										
(1)	74.0	25.2	3.775	9.20 ± 0.96 (6)	124.91	84.74	43.00 ± 4.49	197.1	83.7	1.76
(2)	74.0	25.3	3.725	8.61 ± 0.42 (6)	119.36	81.92	40.39 ± 1.97	202.8	86.1	1.76
(3)	69.5	27.2	3.615	9.75 ± 0.28 (6)	137.78	97.33	47.68 ± 1.37	204.1	86.7	1.97
							mean =	201.3	85.5	
							SD =	3.7	1.6	
							CV =	1.9	1.9	
TBF14.7-1.6 (without funnel-washings)										
(1)	73.5	26.1	3.720	10.33 ± 0.85 (6)	123.83	80.04	49.36 ± 4.06	162.2	68.9	1.81
(2)	73.5	26.2	3.635	9.94 ± 0.35 (6)	145.74	104.37	47.58 ± 1.68	219.4	93.2	1.82
(3)	71.0	27.1	3.740	9.51 ± 0.41 (6)	128.05	87.10	46.43 ± 2.00	187.6	79.7	1.91
							mean =	189.7	80.6	
							SD =	28.7	12.2	
							CV =	15.1	15.1	

TABLE A.III.1 (cont. - 26)

Trap design (replicate)	Flume water height (cm)	Flume water temperature (°C)	V_t (liters)	C_i mean ±SD ( )=N (mg/l)	B_f (mg)	B_t (mg)	B_p mean ±SD (mg)	E	E_r	R_t ($x10^4$)
SERIES 8/24/82 (T_i = 510 sec) (cont.) TBF14.7-1.6 (with funnel-washings)										
(1)	73.5	26.1	3.720	10.33 ± 0.85 (6)	135.80	92.01	49.36 ± 4.06	186.4	79.2	1.81
(2)	73.5	26.2	3.635	9.94 ± 0.35 (6)	156.73	115.36	47.58 ± 1.68	242.4	102.9	1.82
(3)	71.0	27.1	3.740	9.51 ± 0.41 (6)	130.91	89.96	46.43 ± 2.00	193.8	82.3	1.91
							mean =	207.5	88.1	
							SD =	30.4	12.9	
							CV =	14.6	14.6	

APPENDIX IV: Planktonic Larvae May Act Like Passive Particles In Turbulent Near-Bottom Flows

(in press, Limnology and Oceanography)

Abstract

The hypothesis that infaunal polychaete larvae (Mediomastus ambiseta) sink through the water like passive particles in turbulent near-bottom flows was tested in the field using two geometrically different sediment traps. Laboratory flume experiments dictated the a priori prediction that one trap geometry would significantly overcollect larvae relative to the other trap geometry. In field experiments, this a priori prediction was always supported. Thus, Mediomastus larvae may be distributed in near-bottom waters according to the hydrodynamical processes governing the near-bottom distribution of fine suspended sediments. Other processes that could have produced the patterns of larval collections between the trap designs now must be tested against the passive sinking hypothesis. Because the passive sinking hypothesis could not be falsified in these field experiments, considerations of hydrodynamical phenomena must be included in future studies of larval settlement. For example, larvae may first reach the seabed at sites where sediments, with fall velocities similar to larvae, would initially settle.

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Dispersal of most soft-bottom marine infaunal invertebrates occurs during a planktonic larval stage. While large-scale ($\geq$ tens of kilometers) larval dispersal has been assumed primarily a passive process controlled by general oceanic circulation (e.g., Scheltema 1971; Kraeuter 1974; Boicourt 1982; Levin 1983), larval settlement (sensu Scheltema 1974, "the termination of a pelagic larval existence and the assumption of a sessile or nonsessile sedentary life") at very small spatial scales ($\leq$ centimeters) has been presumed primarily an active process where larvae choose their settlement sites based on sediment characteristics (see reviews for laboratory studies of soft-bottom infauna by Meadows and Campbell 1972; Scheltema 1974; Strathmann 1978; and the field studies of Oliver 1979; Williams 1980; Gallagher et al., 1983). Thus, active habitat selection by larvae has long been the favored mechanism to explain correlations between organism and sediment distributions, commonly observed in field surveys of soft-bottom infauna. However, the patterns of species and sediment distributions have been documented for spatial scales (tens of meters to kilometers) that are one to six orders of magnitude larger than the spatial scales (millimeters to a meter, and in one field study, tens of meters) for which active habitat selection has been documented (this literature is reviewed in Hannan 1984).

A mechanism to account for patterns of initial larval settlement must operate at the relatively large spatial scales that apply to sediment transport and deposition while allowing for active habitat selection to occur at much smaller spatial scales. Perhaps the simplest such mechanism is that physical processes determine initial depositional sites for

larvae, just as sites for initial settlement of particulates is hydrodynamically controlled in unsteady ocean flows. (In this study, "initially deposited" is defined as "coming to rest upon the seabed", but does not require accumulation at the deposited locale, as the geological definition of "deposits" implies. In reference to inert particles, "settlement" is synonymous with "initially deposited". For larvae, because "settlement" has the explicit definition given by Scheltema [1974] and reiterated above, "initially deposited" is always used here to indicate that an organism has physically reached the seafloor, but does not necessarily indicate that the organism also permanently terminated its pelagic existence at that time. In essence, "deposited" larvae may or may not have "settled", according to the biological definition of Scheltema.)

The specific hypothesis proposed here is that larvae initially reach the seafloor at sites where particulates (with fall velocities similar to larvae) initally settle. This hypothesis does not require that the deposited organisms remain at these sites. Once larvae are passively deposited over relatively large areas of the seafloor, they may, (1) actively reject the location by swimming into the water column or by remaining at the sediment surface to be resuspended and transported away, (2) be involuntarily resuspended and transported only during storm events, (3) redistribute at smaller spatial scales by actively selecting a microhabitat within that locale, and/or, (4) passively redistribute at smaller spatial scales (e.g., by accumulating around microtopographic structures). Alternatively, larvae may differentially survive in certain microhabitats within the deposited locale.

The hypothesis that larvae sink through near-bottom (within one meter of the seabed) turbulent flows like passive particles was tested in this study. Due to complex biological and physical processes occurring once larvae reach the seafloor, the passive deposition hypothesis cannot be tested by directly sampling the seabed for initially deposited particles and larvae. Thus, the intent of the present study was to determine if larvae that are capable of settlement act like passive particles while suspended in turbulent flows typical of near-bottom current regimes. Determining if larvae sink like passive particles in flows near the bottom is a necessary prerequisite to testing the passive deposition hypothesis. If the passive sinking hypothesis cannot be falsified, then considerations of hydrodynamical processes must be included in all future studies of larval settlement phenomena.

The experimental technique for testing this hypothesis involved using the biased sampling characteristics of sediment traps to collect particles and larvae falling toward the seabed. Traps differentially collect sediments because of self-induced local disturbances to the flow field; this effect is dependent upon trap geometry so that traps of various shapes will collect particles in different relative abundances. By differentially collecting particles, the traps simulate some of the small-scale hydrodynamical processes responsible for transporting and depositing sediments onto the seabed. If larvae are not collected in traps in the rank order of abundance that passive particles are collected, then larvae either are falling through the water into the trap mouths at random (and not according to the hydrodynamics governing passive particle collection by traps) or biological features of the larvae (e.g., behaviors

or physiological responses) determine the collection of larvae by traps. In either case, if hydrodynamical processes do not determine larval collections in traps, then hydrodynamical processes also are unlikely to determine depositional sites for larvae on the seabed. If larvae and passive particles are collected in the same rank order of abundance by the various trap designs, then it is possible that hydrodynamical processes determined the larval collections. However, passive sinking of larvae would not be explicit in this result. If the hypothesis was not falsified, other processes that could have produced the observed patterns of larval collections among the trap designs would have to be tested against the passive sinking alternative hypothesis.

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The specific hypothesis tested in this study is that larvae sinking toward the seabed in the field and passive particles (with fall velocities similar to larvae) sinking in a flume are collected in the same rank order of abundance by several near-bottom trap designs. The results presented here (for two trap designs and for the most abundant

organism collected in the traps) represent only a portion of the experiments carried out in the study; the full study will be discussed in detail in a later paper (Hannan, in preparation). Two designs of traps (differing in geometry, but having the same mouth diameters and similar heights), with different relative particle collection efficiencies, were selected for simultaneous deployment in the shallow subtidal (15 m depth) region of Buzzards Bay, MA (Station 35, described in Sanders et al., 1980). Laboratory experiments demonstrated that one trap design collected significantly more passive particles per unit mouth area than the other; therefore, the a priori prediction for field experiments was that larvae falling passively near the seabed would be similarly overcollected by the one trap design relative to the other.

Laboratory experiments to determine relative particle collection efficiences of various trap designs were conducted in a recirculating freshwater flume with steady, unidirectional flow. The flume was designed and experiments conducted so that neither bottom nor side-wall boundary layers, blockage of flow by traps, or disturbances from the water surface interfered with particle trapping; dynamic and geometric similarity to field conditions also was maintained. Flume experiments are described in detail elsewhere (Hannan 1984).

No scaling of traps was necessary between flume and field experiments because flow speeds tested in the flume (range = 9 to 12 cm/sec; mean = 10.7 cm/sec, measured with an electromagnetic current meter) were within the range of flow speeds measured in the field (range = 0 to 22 cm/sec; for semidiurnal tidal flows measured 0.5- and 1.0-m above the bottom at the study site with Savonius rotors mounted on a bottom tripod

system, described in Butman and Folger 1979). Both flume and field flows had trap Reynolds numbers of the order 10^4, based on trap mouth diameter and water velocity at the height of the trap mouth, so trap Reynolds numbers similarity between flows was maintained. Laboratory flow regimes were not identical to field flow regimes because large-scale turbulence and boundary layer development could not be reproduced in the laboratory. However, local flow-fields and associated turbulent scales (on the order of trap diameter) have the dominant influence on particle trapping (Hannan and Grant 1982; Hannan 1984).

The flume flow was continuously seeded with spherical glass beads (16.0 to 40.2 μm in diameter, density = 2.44 g/cm^3); theoretical fall velocities for these particles are 0.02 to 0.14 cm/sec, as calculated from Stokes' equation (Stokes 1851). Direct laboratory measurements of fall velocities of several species of nonswimming (anesthetized or freshly killed) polychaete larvae were made by timing the descent of individuals through a temperature-controlled water column. For larvae ranging from 300 to 1400 μm in narcotized length, fall velocities (normalized for seawater at 20.4 °C, 30 ppt salinity and one atmosphere) ranged from 0.013 to 0.37 cm/sec; fall velocity was positively correlated with worm size (for $N = 37$, $r_s = 0.65$, significant at $p \leq 0.01$ using the nonparametric Spearman rank correlation coefficient). Glass beads chosen for use in the flume experiments had fall velocities covering the lower range of fall velocities experimentally determined for polychaete larvae; larvae collected in traps at the study site were primarily in the small size range of the larvae used for fall velocity measurements. In flume experiments, to determine average bead concentrations in the

upstream water mass at the height of the trap mouth, water samples were taken at the beginning, midpoint, and end of each trap collecting interval.

One trap was tested in the flume at a time. Particles were collected in traps for 8.5-min intervals. The total weight of beads in traps and in water column samples was used to calculate the relative collection efficiencies of the traps. A predicted estimate of the weight of particles collected by each trap (B_p) was calculated from the following: $(B_p) = (C_i)(T_i)(A_t)(W_c)$, where C_i = mean particle concentration in the water column during trap collection interval, T_i = length of collection interval, A_t = trap mouth area, and W_c = particle fall velocity for the mean bead diameter in the mixture (0.05 cm/sec for a 25 μm bead). The collection efficiency of a trap (E) was calculated as: $(E) = (B_t)/(B_p)$, where B_t is the weight of beads collected by the trap. B_t was corrected for differences in trap volume between trap designs by subtracting out the weight of beads collected in the volume of water initially sampled by the trap when it was uncapped at depth. This was necessary because B_p estimates only particles falling or carried into the trap mouth and not particles that enter the trap in an initial water sample.

Results are reported from three flume and four field experiments for the pair of trap designs used most extensively in the study, a 1.4-liter opaque plastic cylindrical jar 22.7-cm tall and with an 8.4-cm mouth diameter (hereafter referred to as a "standard cylinder") and a 3.8-liter opaque plastic small-mouth (8.4-cm diameter), wide-body (15.3-cm diameter) jar 25-cm tall (hereafter referred to as a "gallon jar"). The mean collection efficiency (E_s) of the standard trap during each

experimental day was used as a normalizing factor for all other trap collections that day yielding relative collection efficiencies (E_r) comparable between experiments (see caption to Figure A.IV.1). Traps screened with fine filament plastic mesh (16-mm^2 openings) and unscreened traps were tested in the flume. Statistical analyses of all experiments were made with Mann-Whitney U tests of the null hypothesis that there is no difference between collections (of particles or of larvae) by gallon jars and standard cylinders.

The flume experiments (Figure A.IV.1) clearly demonstrate that the gallon jars collected significantly more particles per unit mouth area than the standard cylinders. The null hypothesis was rejected at $p \leq 0.05$ for tests between unscreened standard cylinders and unscreened gallon jars on 7/10/82, 7/22/82 and 8/24/82. For tests between screened standard cylinders and screened gallon jars on 8/24/82 the null hypothesis was rejected at $p \leq 0.10$. Thus, the a priori hypothesis for the field experiments is that larvae should be overcollected by the gallon jars compared to collections by the standard cylinders. It is only appropriate to compare the rank order of collections by the two trap designs in the field and in the flume. The quantitative differences in collections between the trap designs depends both on the flow regime and on particle availability. While particles were supplied to the traps at a constant rate in the flume experiments during the steady, unidirectional flow, larval availability in the field is unknown and the tidal flows were unsteady, potentially oscillating between 0 and 22 cm/sec twice daily (Hannan 1984 and B. Butman, personal communication). Thus, the gallon jars are not expected to relatively overcollect larvae in the field

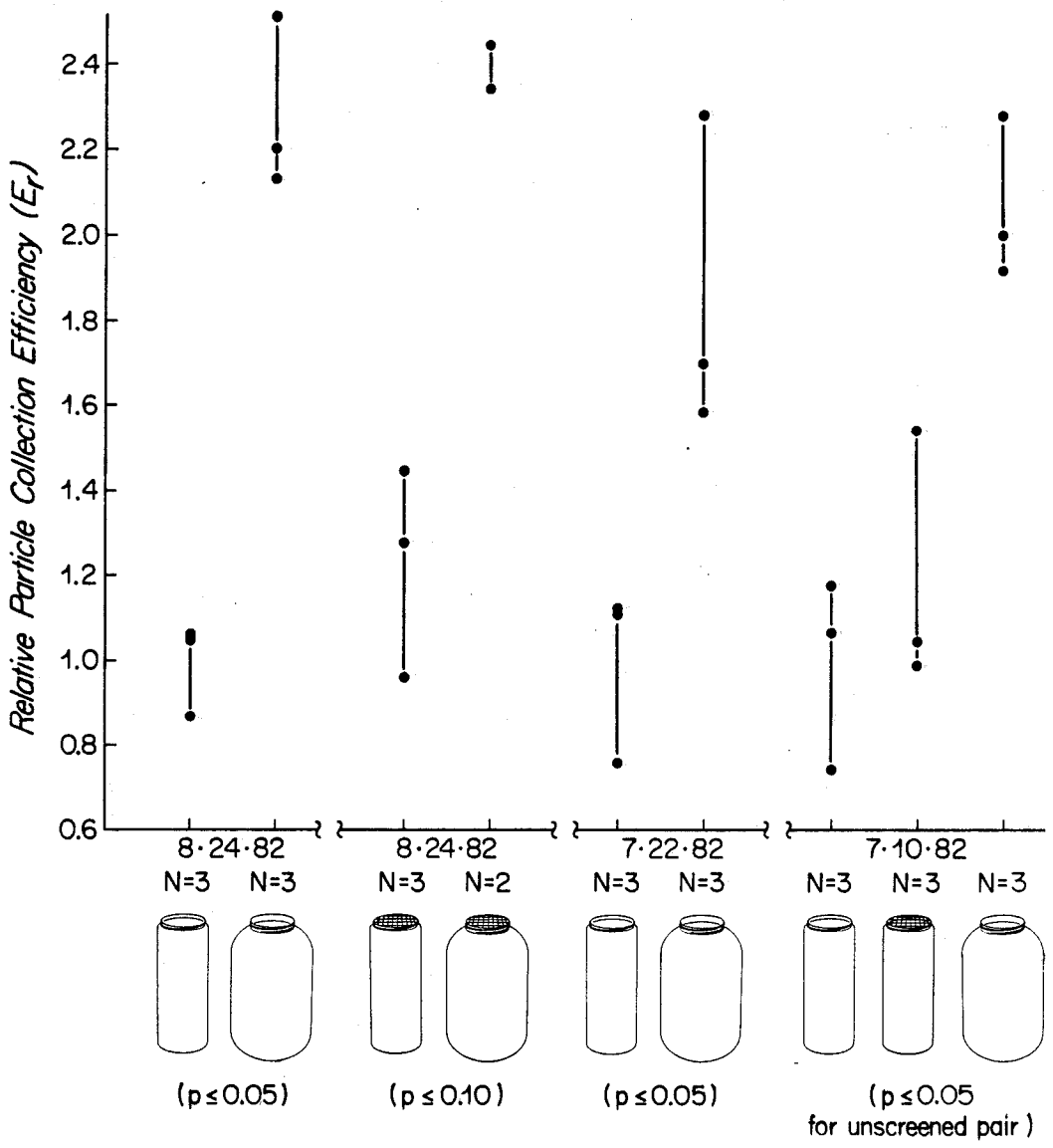

Figure A.IV.1: Relative particle collection efficiencies of standard cylinders and gallon jars in flume experiments. Date of experiment appears below each pair of traps; N = number of replicates. Relative particle collection efficiencies (E_r) were calculated as: $(E_r) = (E)/(E_s)$, where E = efficiency of trap replicate tested (gallon jar or standard cylinder) and E_s = mean efficiency of all standard cylinder replicates tested during that experimental day. Probabilities (Mann-Whitney U tests) for rejecting the null hypothesis (see text) appear below the graph under the pair of traps tested. Cross-hatching over trap mouths indicates the presence of a screen. Vertical lines reflect the entire range of values.

in the same proportion that particles were relatively overcollected by this trap design in the flume. However, as long as some periods of flow correspond with periods of larval availability in the field, the traps are expected to collect larvae in the same rank order of abundance that particles were collected by the traps in the flume.

In field experiments, divers placed each trap (standard cylinders and gallon jars) on a post holding the trap mouth 1.21-m (± 0.3 m) above the bottom and at least 20 trap radii (2.5 to 3.0 m) from an adjacent trap. In all experiments the traps were arranged on the bottom in random order on transects at 2.5- to 3.0-m intervals. Usually three or four replicates of the two trap designs were deployed simultaneously for one to five days. All traps were screened to keep out large motile organisms.

Trap contents were fixed in 5 to 10 percent buffered Formalin, later sieved through nested 500-, 300-, 100- and 63-μm screens into 70 percent ethanol and sorted for larvae. Results are reported here for the capitellid polychaete, Mediomastus ambiseta (Hartman) (hereafter refered to as "Mediomastus") because it was the only species consistently collected in numbers large enough (> 10 larvae/trap) in all four experiments to permit meaningful statistical tests.

The gallon jars collected significantly greater abundances of Mediomastus larvae than did standard cylinders in all four field experiments (Figure A.IV.2), clearly supporting the a priori hypothesis. The null hypothesis was rejected at $p \leq 0.014$ for the 7/27/82 experiment, at $p \leq 0.10$ for the 9/20/82 and 9/22/82 experiments and at $p \leq 0.050$ or 0.10 (see caption to Figure A.IV.2) for the 9/21/82 experiment. The excellent agreement in the number of larvae in replicates of a single

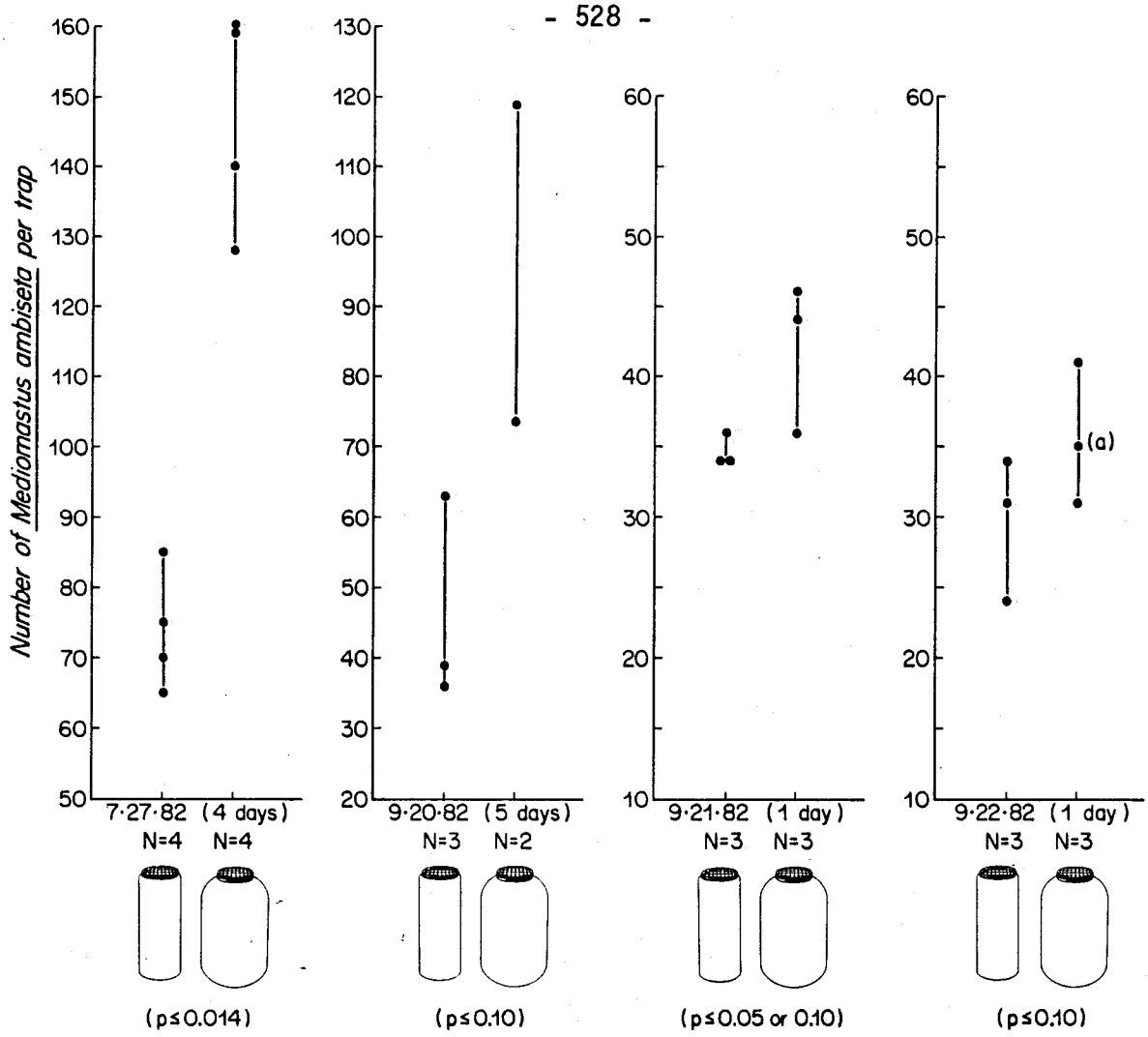

Figure A.IV.2: Number of individuals of Mediomastus ambiseta collected in standard cylinders and gallon jars deployed in the field. Date traps were retrieved from the field and length of collecting interval appear below each experiment; N = number of replicates. Three-quarters of the trap contents (samples split with a standard plankton splitter) in the 7/27/82 and 9/20/82 and the entire trap contents for the 9/21/82 and 9/22/82 experiments were processed for larvae (see text). Probabilities (Mann-Whitney U tests) for rejecting the null hypothesis (see text) appear below the graph under the pair of traps tested. For the 9/21/82 experiment, $p \leq 0.05$ or 0.10 depending on how the tied values are treated. For small numbers of replicates ($N \leq 20$) Siegel (1956) suggests assuming that the tied values are actually different. Assuming the gallon jar actually collected more larvae than the standard cylinder, the null hypothesis is rejected at $p \leq 0.05$, but assuming the opposite, the null hypothesis is rejected at $p \leq 0.10$. Cross-hatching over trap mouths indicates the presence of a screen. Vertical lines reflect the entire range of values. (a) = one tenth of this sample was accidentally spilled before it was sorted so the value plotted here is an underestimate of the number of larvae present in the whole sample.

trap design and the consistently higher mean collections of larvae in gallon jars relative to standard cylinders is remarkable, given the possible sources of error which could enhance both within- and between-trap design variability (capping jars in the field, splitting the samples, washing jar contents into formalin, sieving, and sorting for larvae). Mediomastus individuals collected in traps were considered newly settled postlarvae because they no longer possessed ciliation characteristic of the trochophore larval stage and many individuals were found in tubes. Mediomastus from the traps were essentially all retained on a 100 μm sieve (only 0.8 percent were found in the 300- or 500-μm fractions) while adult Mediomastus in benthic samples are commonly retained on 300- and 500-μm sieves (Sanders et al. 1980; J.F. Grassle, unpublished data).

Absolute differences between mean collections of larvae by gallon jars and standard cylinders were larger during the longer experiments. The simplest explanation for these differences in collections is that over longer intervals it is more likely that periods of current activity which cause measurable biased particle trapping and periods of high larval availability will occur simultaneously, producing large differential collections of larvae between the two trap designs.

Although the observed rank order of larval collections between the two trap designs in the field is the same as the rank order for passive particle collections between the two trap designs in the flume, passive sinking of larvae into these traps is only an implicit and not an explicit result of this study. Larvae and particles may be collected in the same rank order of abundance by the two trap designs for different

reasons. Althernative explanations for the results include the following. (1) The larvae may have actively selected the gallon jar or rejected the standard cylinder due to various aspects of the chemical or sedimentary environments in the traps. (2) The larvae may have actively selected the gallon jar or rejected the standard cylinder due to predators or competitors present in the traps. (3) The larvae may have actively avoided the standard cylinder because of a behavioral response to trap geometry or to water velocities in the vicinity of the trap mouth. (4) The larvae may have been unable to leave the gallon jar, again, due to some behavioral response of the larvae to trap geometry or to water velocities inside the trap.

There is no compelling support for any of these alternative hypotheses at this time. In fact, because differences in collections between trap designs developed even during the one-day intervals, processes associated with the first two hypotheses would have to occur very quickly indeed, for the larvae to perceive differences between the trap designs and make an active choice or die on a time scale of less than one day. Perhaps the strongest support for the passive sinking hypothesis is that fact that when other taxa (bivalve larvae and postlarvae, enteropneust postlarvae, and sabellariid polychaete larvae) were abundant in trap samples, the organisms also were differentially collected acccording to the patterns predicted for passive particles. In addition, five other trap designs nearly always collected Mediomastus and the other organisms mentioned above in the rank order of abundance predicted for passive particle collections (Hannan 1984).

The passive sinking hypothesis could not be falsified for collections

of Mediomastus ambiseta in the field experiments conducted here. Thus, hydrodynamical processes must be included in any future studies of processes that determine patterns of initial larval settlement. Other processes that could have produced the observed patterns of Mediomastus collections between the trap designs now must be tested against the passive sinking alternative hypothesis. However, information is required on various aspects of the biology and ecology of Mediomastus larvae before such process-oriented experiments can be designed.

If larvae sink like passive particles to heights of about one meter above the seabed, as the results of this study suggest, then it is possible that larvae initially reach the seafloor at sites where particulates, with fall velocities similar to larvae, initially settle. Detailed laboratory flume experiments are necessary to unequivocally determine if larvae continue to fall through the lowest meter of water (i.e., below the trap location in the field) like passive particles and are then passively deposited onto the sediment surface. However, it is only within a few centimeters from the bed that the range of speeds and other characteristics of flows may differ significantly from the flow processes occurring at the trap height. Two reasons for this are that, typically, the near-bottom ($\leq$ 1 m) velocity profile is expected to be logarithmic in the field, so flow speeds would not decrease appreciably until very near the bed, and even at the trap height, the range in flow speeds regularly includes zero or near-zero values, because the flows are primarily tidal at the study site.

Flume experiments are also needed for determining if, once larvae are passively distributed in near-bottom waters at the spatial scales

($\leq$ tens of meters) applying to fine suspended sediment distributions, they can then actively select initial settlement sites at the very small spatial scales ($\leq$ centimeters) tested in laboratory (e.g., Wilson 1952, 1977; Gray 1966) and in field (e.g., Oliver 1979; Williams 1980; Gallagher et al., 1983) experiments. In addition, sites where larvae are initially deposited may differ from sites where postlarvae eventually recruit into populations. As previously stated, after initial deposition, larvae or postlarvae may choose microenvironments within a given location, they may actively reject the location by swimming into the water column, they may choose to remain at the sediment surface to be resuspended or resuspension may be involuntary, but, in either case, the organisms could be transported to new locations regularly (Bell and Sherman 1980; Palmer and Brandt 1981; Hagerman 1981) or only during storm events (Hogue 1982; Dobbs and Vozarik 1983), and/or the larvae may accumulate passively around microtopographic structures (Eckman 1979, 1983). Alternatively, larvae initially deposited over a large area may differentially survive in hospitable microenvironments within that locale. Results of the present study distinctly underscore the necessity of routinely including considerations of small-scale hydrodynamical processes in studies of the ecology of soft-bottom marine systems.

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